The Reproductive Cycles of Western and Mountain Hemlock

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PREFACE

British Columbia has 25 native conifer species, of which 15 are commercially important and scheduled for reforestation. Tree improvement programs for four of these species are now under way and programs for several other species are planned. A necessary prerequisite for extensive reforestation and tree improvement programs is a complete understanding of the reproductive cycle of each species.

Until 1970, Douglas-fir was the only native species for which the complete reproductive cycle was known. Since that time, studies of the reproductive cycles have been completed for 13 of the other commercially important conifers of British Columbia. These studies include descriptions of vegetative bud and shoot development as they relate to cone initiation, the time and method of cone initiation, predormant and postdormant cone-bud development, pollen development, pollination, and embryo and seed development. Although these studies provide essential details of the reproductive cycles, a more general description of all aspects of the reproductive cycle of a particular species is frequently requested.

This request has resulted in a series of short books concerning the reproductive cycles of several conifers. Serving as ready references for foresters and others concerned with seed production and tree improvement, these books will explain the complete reproductive cycle; provide useful guidelines for cone induction studies; assist in forecasting pollen and seed production; enable more effective pollination; and provide some clues to the causes of poor seed production. In addition, such information should be useful to students of forestry and biology at universities, technical schools and high schools.

This book, *The Reproductive Cycles of Western and Mountain Hemlock*, is not meant to include a complete literature review. Only the most pertinent and accessible references are cited and listed, providing a source for numerous related reports.

ACKNOWLEDGEMENTS

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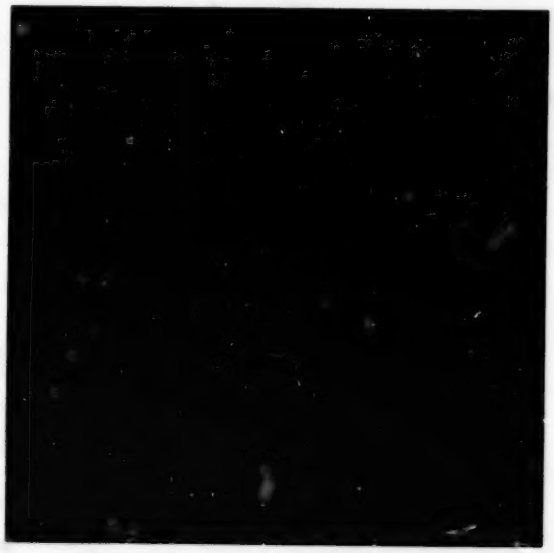
The Reproductive Cycles of Western and Mountain Hemlock



Introduction

The hemlocks, genus *Tsuga*, are members of the largest family of conifers, the Pinaceae. There are 10 to 14 species of hemlocks. Four are North American, two occurring in the west and two in the east, while the other species occur in temperate regions of the Himalayas, China, Taiwan, and Japan (Fowells (compiler) 1965; Dallimore and Jackson 1966). Three species of hemlock grow in Canada. Western hemlock, ***Tsuga heterophylla*** (Raf.) Sarg., and mountain hemlock, ***Tsuga mertensiana*** (Bong.) Carr., are mainly west coastal species although both have a limited distribution in the interior of British Columbia, Washington, Idaho, and Montana. Eastern hemlock, ***Tsuga canadensis*** (L.) Carr., ranges along Canada's southern border from western Ontario to Cape Breton Island, and southward in the United States to the mountains of Georgia.

Taxonomy

The hemlocks are classed into two sections based on differences in leaves, cones, and pollen. The section Micropeuce contains all but one or two living species which, like western hemlock (Fig. 1), have leaves that are flat and 2-ranked, small seed cones, and pollen without wings. The section Hesperopeuce, represented only by mountain hemlock (Fig. 2) and possibly one other species from China, has radially arranged leaves, large seed cones, and winged pollen (Dallimore and Jackson 1966). Fossil records from Europe and central Asia show that many different species of hemlock once grew in these regions, too, and that species within the Hesperopeuce were once about as numerous and widespread as those of the Micropeuce are today (Florin 1963). It is believed that members of the Micropeuce were derived from the more ancient members of the Hesperopeuce (Taylor 1972).

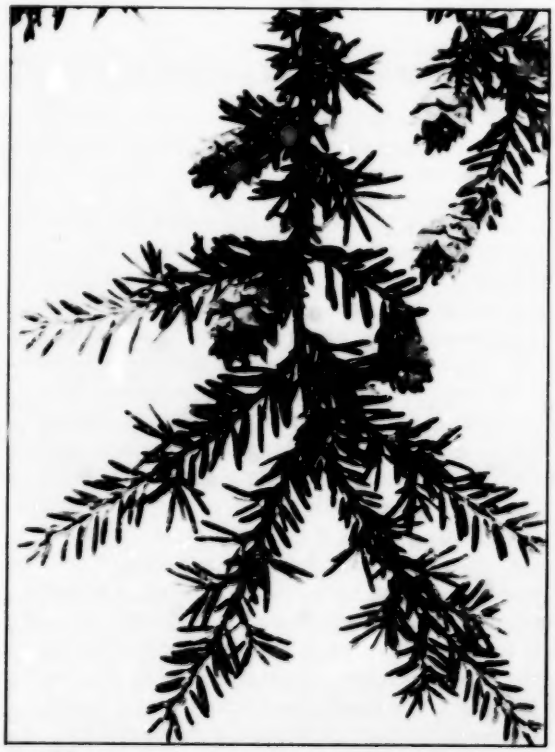


FIGURE 1. Western hemlock branch and mature, open cones. (X 1/2)

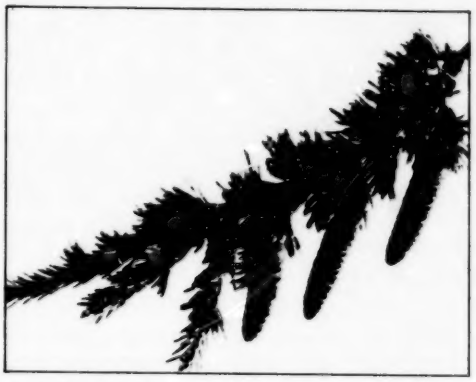


FIGURE 2. Mountain hemlock branch and mature, but closed, cones. (X 1/3)

The uniqueness of mountain hemlock among better-known living hemlocks has intrigued foresters and botanists for many years. In extensive studies of herbarium and arboretum specimens, French workers compared characteristics of western and mountain hemlocks with those of Sitka spruce (*Picea sitchensis* (Bong.) Carr.), and found that mountain hemlock resembled Sitka spruce in more respects than it did western hemlock. Based on these results, they suggested that mountain hemlock evolved as a hybrid between western hemlock and Sitka spruce at some unspecified time and location (Campo-Duplan and Gaussen 1948). However, in their proposal they failed to consider the numerous other Hesperopeuce hemlocks represented in the fossil record, and their possible origin; and they neglected to consider whether mountain hemlock and Sitka spruce inhabited the same area at the time of the proposed hybridization. More recent embryological studies show western hemlock (Stanlake and Owens 1974) and mountain hemlock (Owens and Molder 1975) to be essentially the same and to differ in important aspects from Sitka spruce (Owens and Molder 1980). Furthermore, there is an absence of backcrosses and hybrid swarms of western hemlock and Sitka spruce in the field (Duffield 1950), and attempts at hybridization have failed (Meagher 1976). For these reasons the proposed hybrid origin for mountain hemlock seems unlikely.

Distribution and Habitat

Western hemlock (Fig. 3) is primarily a coastal species, distributed in a narrow band from Alaska to Northern California. It also grows in a disjunct pattern in the humid interior of British Columbia, northeastern Washington, northern Idaho, and northwestern Montana. It is mainly a low-elevation coastal species that grows best between sea level and 600 m in coastal regions, though it may extend up to nearly 2000 m elevation in the Rocky Mountains (Fowells (compiler) 1965; Hosie 1975). At the higher elevations it is usually associated with mountain hemlock and sub-alpine fir (*Abies lasiocarpa* (Hook.) Nutt.). Western hemlock is very shade tolerant but sensitive to dry soils and frost. It grows best in areas with high rainfall and moderate temperatures, but it can withstand minimum temperatures of -47°C in the interior and -25°C on the coast, and maximum temperatures of 38°C if soil moisture is adequate (Packee 1976).

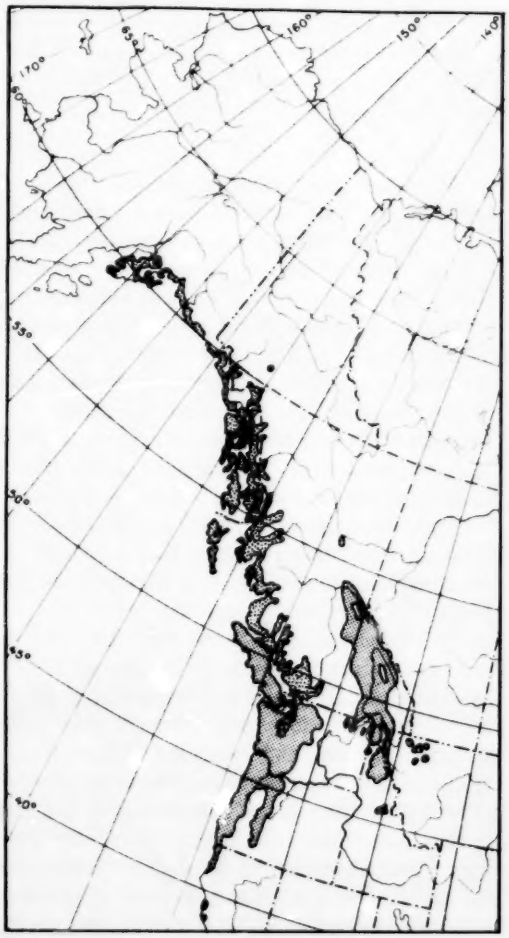


FIGURE 3. Distribution of mountain hemlock. (Reproduced from Little, 1971.)

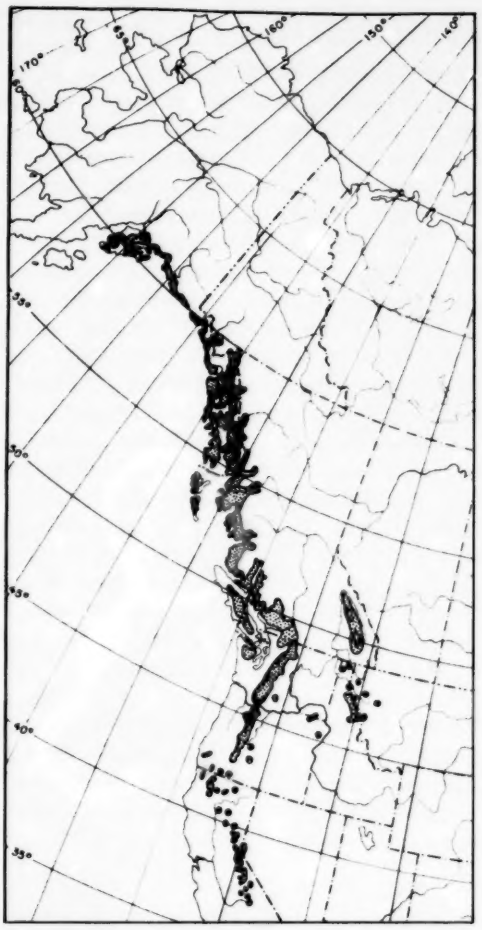


FIGURE 4. Distribution of western hemlock. (Reproduced from Little, 1971.)

Mountain hemlock (Fig. 4) is a coastal species in the northern part of its range, Alaska to southern British Columbia. It commonly occurs near sea level, but is usually found between 1000 m and 1500 m in British Columbia. In the southern part of its range, through the Cascade and Sierra Nevada mountains, to central California, the species occurs at higher elevations — as it does in southeastern British Columbia, northern Idaho, and northwestern Montana (Fowells (compiler) 1965). In the Cascade mountains it grows between 1200 and 2100 m, and in the Sierra Nevada mountains of California it grows at elevations up to 3350 m. At the higher elevations it occurs as individual trees or as scattered clumps. Like western hemlock, it is shade tolerant and moisture-demanding. It occurs commonly in areas that are covered in early autumn by heavy, wet snow which may remain until late July (Packee 1976). It is able to withstand more extreme winter temperatures than can western hemlock and it commonly has a shorter growing season. At higher

elevations mountain hemlock is commonly associated with sub-alpine fir (Franklin 1962; Fowells (compiler) 1965).

Economic Importance

There is no distinction made commercially between western hemlock and mountain hemlock. Despite their rather limited distribution in British Columbia, hemlocks rank third in volume of species cut annually, just behind lodgepole pine and interior spruce. Approximately 85% of the hemlock cut is from coastal areas (B.C. Ministry of Forests 1981, 1982). Hemlocks are used extensively for pulpwood, but other uses include lumber for general construction and plywood. Its fine grained, resin-free wood makes it a suitable lumber for finishing. The wood is generally very wet and often difficult to dry (Hosie 1975).

Western hemlock is commercially more important than mountain hemlock because the former displays more rapid growth and larger size, is more extensively distributed, often forms purer stands, and generally is more accessible. Mountain hemlock is an important sub-alpine species in many locations where few other conifers survive. There it serves as a protective cover for watersheds, as a wildlife habitat, and as a major component in the long-term maintenance of the sub-alpine environment.

Reproductive Potential

Western hemlock at lower elevations is generally a good cone and seed producer. Cones may form on open grown trees less than 20 years old, but good cone crops usually do not occur until trees are between 25 and 30 years old. Seed cones are commonly borne in upper regions of the crown but can occur abundantly throughout the crown in open grown trees. Individuals usually produce some cones every year and heavy (collectable) cone crops every three or four years. Seed cones are small, about 2 cm long (Fig. 1), and can produce up to 30 or 40 seeds (Fowells (compiler) 1965). The number of filled seeds, however, ranges from fewer than 10 to approximately 20 per cone (Meagher 1976).

Mountain hemlock is also considered to be a good seed producer. Some trees begin to bear cones by the time they are 20 years old. Seed cones are commonly restricted to upper regions of the crown where, in years of heavy cone crops, they will weigh down the branches (Fowells (compiler) 1965). Open grown trees may bear seed cones throughout the crown. Individuals may produce some cones every year but heavy (collectable) cone crops occur infrequently, every two to eight years (Dobbs *et al.* 1976). In many wet sites heavy cone crops are rare. Seed cones are large, about 5 cm long (Fig. 2) with approximately 100 seeds per cone. Good estimates for the number of filled seeds per cone are not available.

Western hemlock can regenerate rapidly in shaded, moist, cool sites (Williamson 1976), whereas natural regeneration of mountain hemlock in sub-alpine regions is very slow. The extensive harvesting of these species will not permit natural regeneration to occur fast enough in many areas. As a result, extensive reforestation is planned, requiring a constant supply of high quality, yet economical seed. In response to this need, tree improvement programs and seed orchards have been started for western hemlock in coastal B.C., although similar work has not been started for mountain hemlock. It is expected that successful operation of seed orchards can be facilitated when the complete reproductive cycles of both species is understood by operators. Such understanding must include the important events that occur during a 15- to 16-month period: from the time of cone initiation in the late spring and early summer, through pollination of these cones the following spring, until seeds are mature and shed in the fall of the same year that the cones were pollinated (Fig. 5).

Vegetative and Reproductive Phenology

The growth cycles of vegetative buds and cones of western and mountain hemlocks are essentially the same in most anatomical details (Owens and Molder 1973, 1974; Stanlake and Owens 1974; Owens and Molder 1975; Owens 1984*a*, 1984*b*). The main difference is in phenology of vegetative and reproductive development. Although the phenology is similar at moderate elevations, where both species can occur, it differs considerably when low-elevation western hemlock (Fig. 5) is compared with moderate- or higher-elevation mountain hemlock. These differences are detectable only at the beginning and end of the growth cycle, when inconspicuous internal — but not external — changes occur. Events nearer the middle of the growth cycle vary less in phenology (Fig. 5).

Although the phenology may vary, the sequence and many of the details of vegetative and reproductive development are the same for both species. Consequently, a single description of the more common western hemlock is provided (Fig. 5). Differences that occur in mountain hemlock will be described in various sections of the text.

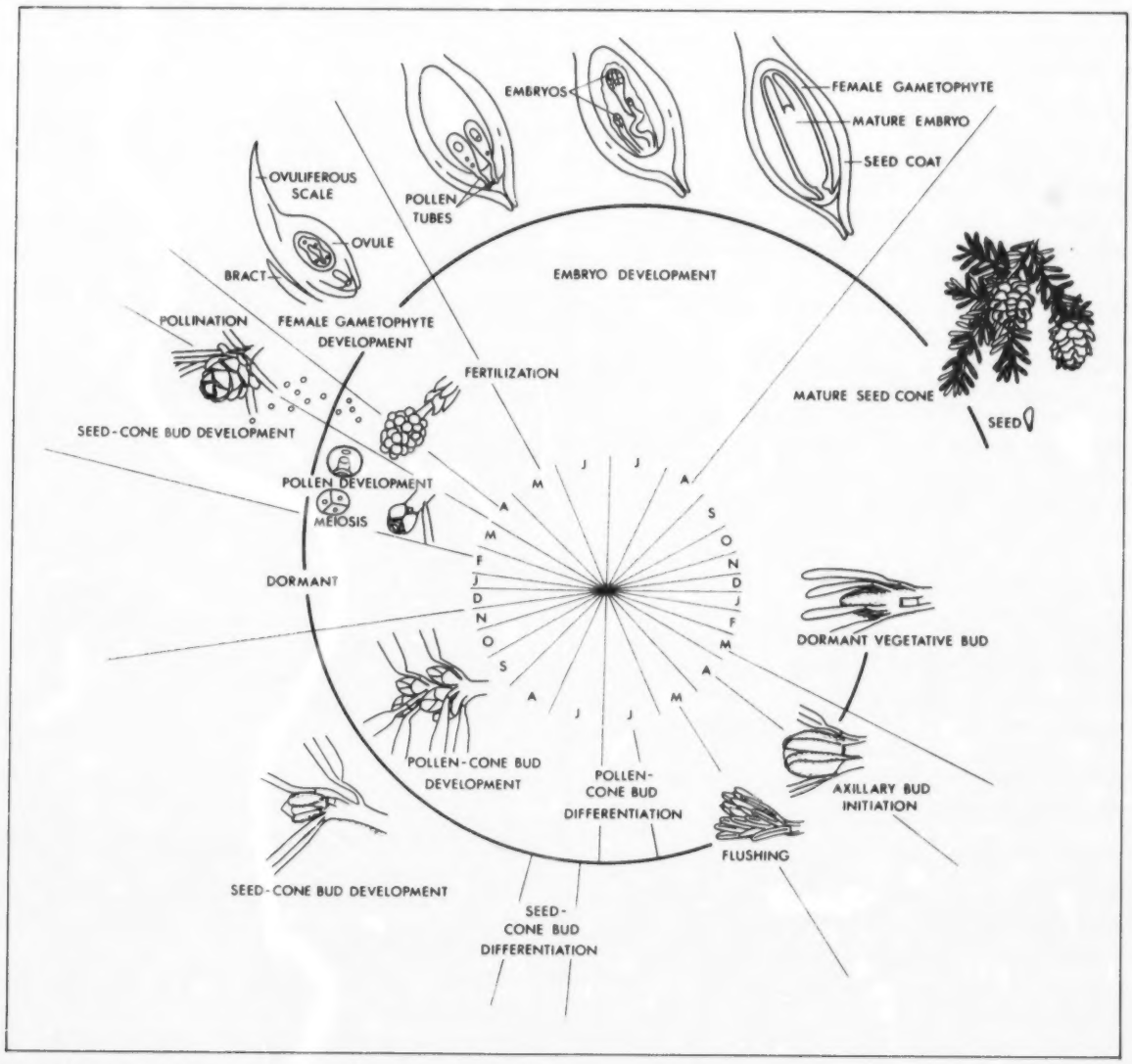


FIGURE 5. The phenology of vegetative and reproductive buds and cones of western hemlock.

Vegetative Bud and Shoot Development

Vegetative bud development of trees from northern or high-elevation regions begins later in the spring and stops earlier in the fall than in trees from southern or low-elevation regions. A typical example of coastal western hemlock's development is shown in Figure 6. In western hemlock vegetative bud development lasts almost nine months, from late March to mid-November. In mountain hemlock growing at about 1000 m elevation, vegetative bud development lasts about six months, from mid-April to mid-October (Owens 1984*a*). Although the same bud-scale and leaf structures are initiated during these periods, where the growing season is short, fewer structures are initiated and at a faster rate than when the growing season is long.

The dormant vegetative bud consists of brown, leathery, outer bud scales that are more hairy in western than in mountain hemlocks; and thin, papery, white, inner bud scales. Bud scales enclose the preformed embryonic vegetative shoot. This shoot usually bears all of the next season's embryonic leaves ("leaf primordia") (Figs. 6*A*, 7, 8). When vegetative bud growth begins in the spring, the telescoped shoot axis and leaf primordia elongate, causing the bud to swell (Fig. 6*H*), and then burst ("flush") through the bud scales (Fig. 6*I*). The time of bud flush is quite variable with latitude, elevation and provenance, and

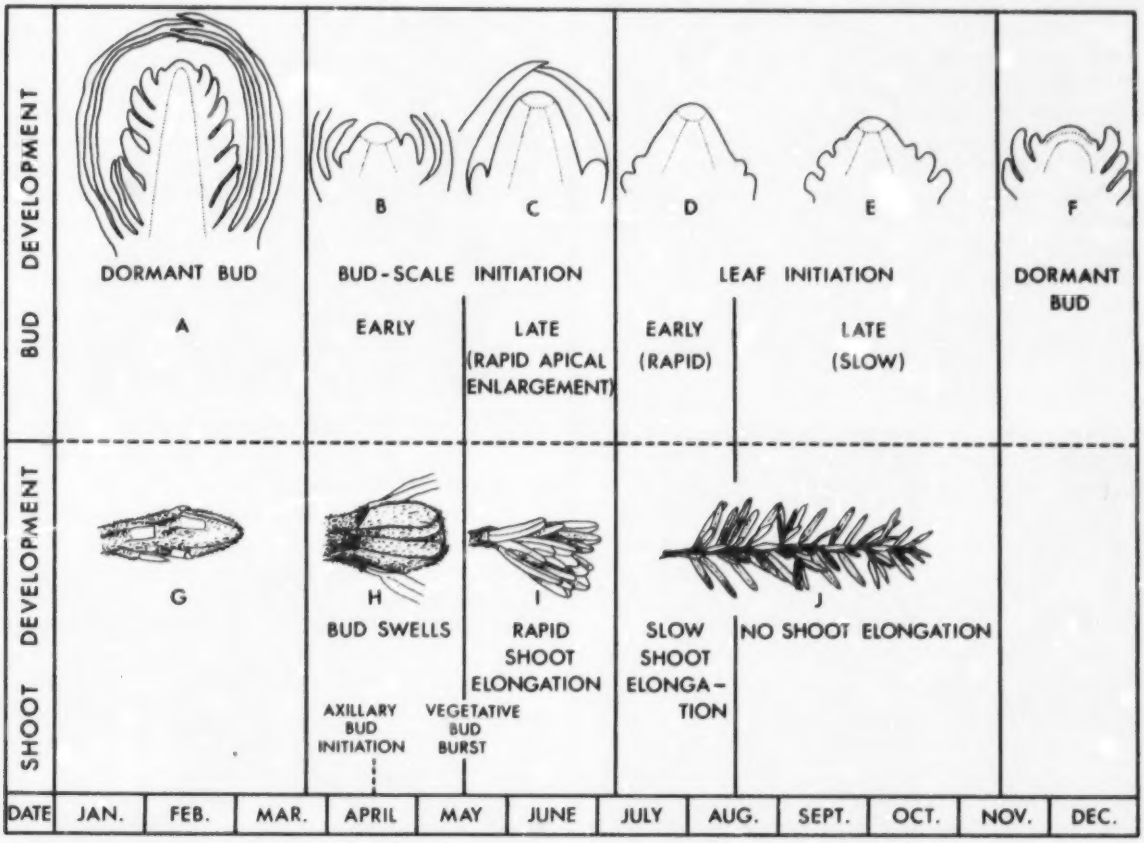


FIGURE 6. The phenology of vegetative bud and shoot development of coastal western hemlock (Owens and Molder 1973).

is affected by temperature and soil condition during early bud development (Meagher 1976). Warmer temperatures speed bud development, causing buds to flush earlier. Vegetative buds of coastal western hemlock commonly burst in May (Fig. 6), approximately one month before those of higher elevation mountain hemlocks (Owens and Molder 1973; Owens 1984*a*).

FIGURE 7. Scanning electron micrograph of a dormant vegetative terminal bud after removal of bud scales. Most leaf primordia (LEAVES) have been initiated. (X 40)

FIGURE 8. Median longitudinal section of a dormant vegetative terminal bud showing the apical meristem (AM), leaves and bud scales. (X 25)

Flushing is followed by a period of rapid, then slow, shoot elongation, and finally by a period of shoot maturation when no lateral shoot elongation occurs. During this time, leaf and shoot tissues mature and complete development (Fig. 6*J*). Bud development, though hidden by bud scales, continues throughout the growing season. As the vegetative buds are swelling, new lateral buds are initiated in the leaf axils (just above the juncture of the leaf primordium and the embryonic stem) of some leaf primordia (Fig. 9). These tiny buds begin as an indistinct mound of cells, but enlarge rapidly and take on the same appearance as the terminal apical meristem on the shoot (Fig. 10).

The apical meristems of the terminal and new

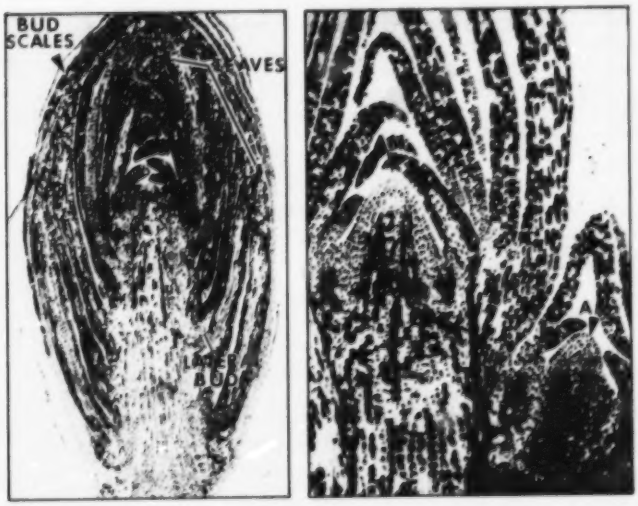


FIGURE 9. Median longitudinal section of a vegetative terminal bud during bud swelling when new lateral buds are being initiated. (X 20) LEFT

FIGURE 10. Median longitudinal section of a large vegetative terminal and smaller lateral bud showing the apical meristems (AM) during bud-scale initiation. (X 32) RIGHT

lateral buds then undergo a predictable sequence of developmental events (Figs. 6*B-F*) that correlate with lateral shoot development (Figs. 6*H-J*). During lateral shoot elongation the terminal and lateral meristems initiate a spiral of bud scales that protect the apical meristems (Figs. 6*B*, 6*C*, 10, 13). Near the end of the period of lateral shoot elongation, the apical meristems enlarge rapidly (Fig. 6*C*), and then initiate a spiral of leaf primordia up the flanks of the apical meristem (Fig. 6*D*). This begins in early July in western hemlock (Fig. 6) and at the end of July in mountain hemlock. Leaf primordia are initiated rapidly in both species until late August by which time about two-thirds of the final number of leaf primordia are started (Fig. 11). Thereafter, leaf primordia are initiated more slowly until the vegetative buds become dormant, in mid-October for mountain hemlock, and mid-November for western hemlock (Fig. 6) (Owens and Molder 1973; Owens 1984*a*).

FIGURE 11. Scanning electron micrograph of a vegetative terminal bud during leaf initiation in late August. (X 70)

A variation of this developmental sequence occurs on vigorous vegetative shoots of western hemlock. On these shoots newly initiated lateral bud primordia located in the distal part of the shoot may initiate two or more leaf primordia before they begin bud-scale initiation. The internodes between these leaves elongate immediately, raising the apex from its axillary position. This short period of "free growth" produces lateral buds at the ends of short shoots. The apical meristem then begins the normal sequence of bud-scale initiation, leaf initiation and dormancy as shown in Figure 6. This process has not been observed in mature mountain hemlock trees (Owens 1984*a*).

Terminal buds are usually larger and have more bud scales and leaf primordia than axillary buds (Fig. 12). More bud scales result because terminal buds are more vigorous and have a longer period of bud-scale initiation than do axillary buds. Lateral buds are less vigorous and form fewer leaf primordia the closer they are located to the base of the shoot on which they develop. Some lateral buds stop development, the apical meristem degenerates, and the buds abort. Development of other lateral buds becomes arrested

FIGURE 12. Scanning electron micrograph of a small, dormant, vegetative lateral bud with few leaves. (X 95)

during bud-scale initiation and they remain as small, latent buds that can resume development at some future date by forming leaf primordia and elongating into epicormic shoots.

After winter dormancy, terminal and lateral buds begin growth at approximately the same time. They repeat the same cycle that the terminal apex passed through the previous year (Fig. 6). Some vigorous terminal buds, and some vigorous, distal, lateral buds of western hemlock have a slightly altered cycle. They begin development with a period of leaf initiation before they begin bud-scale initiation. This results in a variable period of "free growth" in the early spring, during which the shoot axis elongates and, simultaneously, leaf primordia are initiated. As a result, the number of leaves formed for that year's shoot may increase although this has not been observed in mature mountain hemlocks (Owens 1984*a*).

Differentiation of Bud Types

Cone buds of western and mountain hemlock generally develop on lateral shoots of moderate vigour, rather than on leader shoots or vigorous lateral shoots. Seed-cone buds always form from the terminal bud on a lateral vegetative shoot. Pollen-cone buds form occasionally from terminal buds, but most frequently from newly initiated lateral buds. Consequently, seed cones are terminal on the ends of vegetative shoots that are one or two years old (Figs. 1, 2, 21), and pollen cones are generally lateral (Fig. 23). In both instances cone buds differentiate (i.e. become anatomically distinct) after all of the bud scales have been initiated. At that time the apical meristem (Fig. 13) may initiate leaf primordia and become a vegetative bud as described in the previous section (Fig. 6); or it may become reproductive and initiate either bracts to become a seed-cone bud, or "microsporophylls", to become a pollen-cone bud (Figs. 16, 17). Biochemical differentiation of buds may begin earlier than anatomical differentiation, but this has not been studied in hemlocks.

Stages of differentiation, from the initiation of the last bud scales (Fig. 13), to the initiation of leaves, bracts (Fig. 15), or microsporophylls (Fig. 14), occur during a two-week period and are only visible microscopically. The reproductive apical meristems undergo more cell divisions and enlarge more quickly than vegetative apical meristems. As well, the new leaves, bracts, and microsporophylls have slightly different shapes, which helps in the early microscopic distinction of bud types. However, these methods of early identification of buds are too tedious for routine work, and it is much easier to wait until late summer when buds can usually be distinguished on the basis of external characteristics. (See the section "Identification of Buds", page 16.)

Bud differentiation in western hemlock (Fig. 16) and mountain hemlock (Fig. 17) occurs at about the same time when they are grown in similar locations (Owens and Molder 1973; Owens 1984*a*). The time of bud differentiation can be estimated for trees from various locations because it usually occurs at the end of the elongation period of the lateral shoots on which each type of cone bud will form. However, shoots bearing pollen-cone buds elongate very little after flushing, so it is difficult to estimate the time of differentiation based on the amount of shoot elongation. Also, leader shoots and vigorous lateral shoots may have longer periods of shoot growth. The end of their elongation period does not correlate with the time of cone bud differentiation.

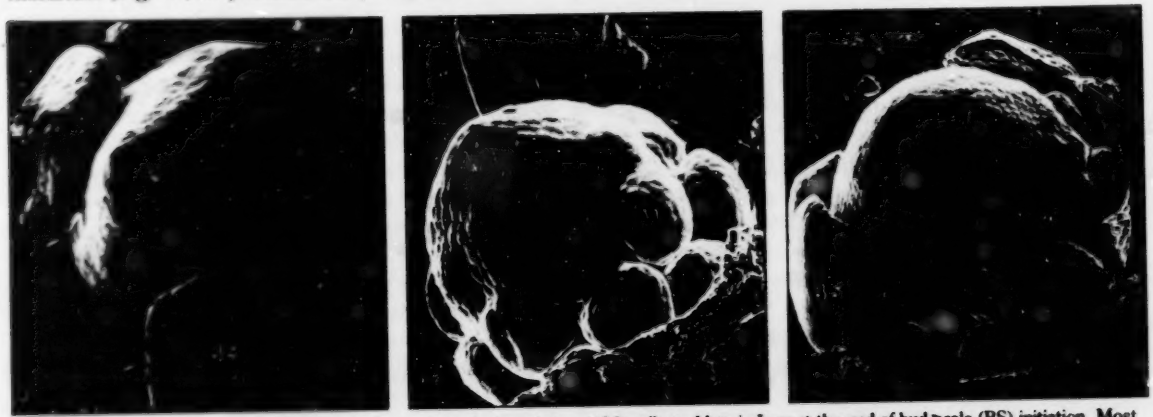


FIGURE 13. Scanning electron micrograph of a conical apical meristem (AM) collected late in June at the end of bud-scale (BS) initiation. Most bud scales have been removed. (X 125). LEFT

FIGURE 14. Scanning electron micrograph of a pollen-cone apical meristem (AM) collected during early stages of microsporophyll (M) initiation. All bud scales have been removed. (X 100) CENTRE

FIGURE 15. Scanning electron micrograph of a seed-cone apical meristem (AM) collected at the beginning of bract (B) initiation. Most bud scales (BS) have been removed. (X 80) RIGHT

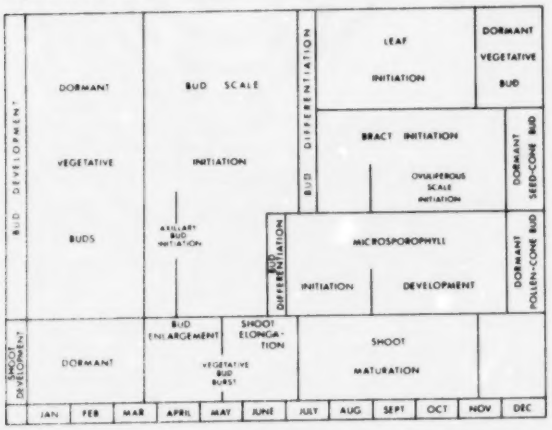


FIGURE 16. The times of bud differentiation and development in western hemlock. (Redrawn from Owens and Molder 1974.)

In western hemlock pollen-cone buds begin to differentiate in late June (Fig. 16), and seed-cone buds begin to differentiate two to three weeks later, in early July (Fig. 16). Cone-bud differentiation is followed by approximately four months of cone-bud development, during which time all microsporophylls, bracts, and most ovuliferous scales are initiated. Cone buds become dormant about the end of November in coastal western hemlock (Fig. 16) (Owens and Molder 1973).

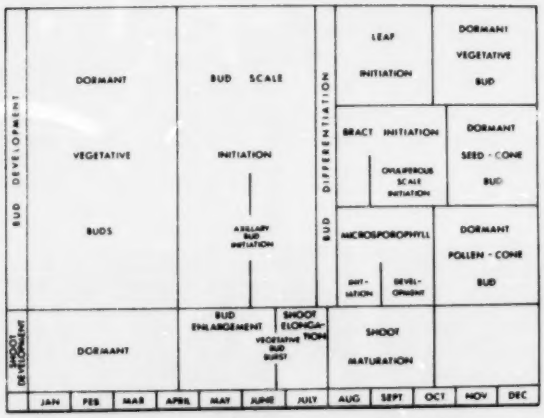


FIGURE 17. The times of bud differentiation and development in mountain hemlock. (Redrawn from Owens 1984*b*.)

In mountain hemlock pollen-cone buds and seed-cone buds begin to differentiate at the same time, in late July (Fig. 17).

Differentiation is followed by two months of cone-bud development during which all microsporophylls, bracts, and most ovuliferous scales are initiated. Cone buds become dormant in mid- to late October in mountain hemlock growing at moderate elevations (Fig. 17) (Owens 1984*b*).

Pathways of Bud Development

Seed-cone buds in western and mountain hemlocks are terminal on lateral shoots that are one or more years old. These lateral shoots develop from vegetative lateral buds. Although the number of vegetative lateral buds initiated varies little from year to year, the pathway of their development in subsequent years can vary. In one year, on a particular tree, almost all lateral shoots remain vegetative. In another year on the same tree, many of the apical meristems of lateral shoots will initiate bud scales, undergo a differentiation phase, and then initiate bracts and ovuliferous scales rather than leaves. In both years the time and method of bud-scale initiation are the same and differences between vegetative and seed-cone buds do not begin to appear until the time of bud differentiation (Fig. 15) (Owens and Molder 1974; Owens 1984*b*).

The number of pollen-cone buds formed in western and mountain hemlocks is determined primarily by the pathway of development of the newly initiated lateral buds. In some years, all of these lateral buds will stop development during bud-scale initiation. Some will stop development very early, abort, and degenerate, leaving no evidence of their existence. Others will stop development after many bud scales are initiated. The apical meristem of these buds may abort, leaving an empty bud, or the development of the apical meristem may become arrested, forming a small, prematurely dormant, latent bud rather than a pollen-cone bud. The latent buds may abort during winter or occasionally, at least in western hemlock, resume development the following spring and differentiate into pollen-cone buds (Fig. 23) (Owens and Molder 1974; Owens 1984*b*).

Terminal buds on the short, pollen-cone bearing shoots usually remain vegetative. However, in western hemlock, and less commonly in mountain hemlock, terminal buds may initiate bud scales, and then differentiate into a pollen-cone bud. This is more common in a year when few pollen-cone buds differentiate. In a year when many pollen-cone buds differentiate, nearly all lateral buds, some terminal buds, and as well, some of the previous year's latent buds, may differentiate into pollen-cone buds. As a result, pollen-cone buds can form profusely on very short shoots, forming a cluster of buds near the base of the shoot (Figs. 23, 25, 26) (Owens and Molder 1974; Owens 1984*b*).

When the terminal bud on a shoot differentiates into a seed-cone bud or a pollen-cone bud, the vegetative growth of the shoot ends. However, on seed-cone bearing shoots, a lateral bud below the terminal cone may develop into a vegetative shoot after the seed cone has matured.

Enhancing Cone-Bud Differentiation

The number of cone buds depends on the proportion of developing terminal or lateral buds which become reproductive (Owens and Molder 1974; Owens 1984*b*). However, the physiological processes that control the differentiation of terminal and lateral apices in conifers are poorly understood. Environmental factors that enhance the number of cone buds in the Pinaceae include abundant sunshine, warm temperature, and low rainfall preceding and during the time of cone-bud differentiation (Puritch 1972). These conditions have been correlated with abundant cone-bud formation in a stand (or a heavy cone crop the following season).

Many methods of enhancing cone-bud differentiation have been tried in conifers (Puritch 1972), but most have given variable results depending upon the species, timing of treatments and methods used. Combinations of treatments can enhance cone production even more. Many treatments cause some form of stress within the tree, resulting in "stress" crops. Some treatments, if not properly applied, may result in permanent injury to the tree, and injuries inflicted by nature can also cause stress crops.

Plant growth regulators (hormones) have been used to induce cones in juvenile conifers, or to enhance cone production in reproductively mature trees (Puritch 1972; Pharis and Ross 1976; Ross and Pharis 1981; Ross *et al.* 1983). Early attempts used gibberellins A_3 (GA_3). It induced flowering in some species of the Cupressaceae and Taxodiaceae but not in the Pinaceae. More recently, the less polar gibberellins (GA_4, GA_5, GA_7 and GA_9) have been used in varying combinations to induce cone buds ("flowering") in several species of the Pinaceae, including western hemlock (Ross *et al.* 1981; Brix and Portlock 1982).

FIGURE 18. Western hemlock juvenile tree showing seed cones (arrow) induced by $GA_{4/7}$ in combination with drought treatments.

Western hemlock has proven to be an ideal subject for $GA_{4/7}$ treatments and has given excellent and consistent cone crop response under a variety of experimental conditions and tree ages. Cones have been induced on 1- to 5-year old potted seedlings (Fig. 18) (Puritch 1972; Brix and Portlock 1982), 6-year-old field-grown seedlings, and 7- to 8-year-old field-grown rooted ramets (Puritch 1972). Treatments of potted trees were most effective where GA treatments were coupled with water stress treatments applied in late June and early July, before the natural time for anatomical differentiation of cone buds (Fig. 16).

Although for many Pinaceae species $GA_{4/7}$[1] is more efficiently and effectually applied by stem injection, western hemlock is highly responsive to spray treatments (Puritch 1972). $GA_{4/7}$[2] has been applied as a foliar spray at a concentration of 200 mg/L. A surfactant of 0.05% AROMOX-C12W[3] has been used to increase uptake through the leaf surface. Best results can be obtained if plants are sprayed once per week for six weeks starting at vegetative bud burst. For mature vegetative propagules, $GA_{4/7}$ treatment alone gives good results. Its efficacy, however, is enhanced by water stress and calcium nitrate fertilizer. For seedlings, cone induction has been obtained using $GA_{4/7}$ as above, with water stress. Water stress can be applied in potted trees by withholding watering so that the soil is kept reasonably dry to the touch. Since western hemlock is very sensitive to water stress, this must be carefully monitored to prevent partial or complete defoliation. Water stress is most easily measured with a pressure bomb. Water should be withheld until a predawn water stress of -10 to -12 bars is reached[4]. Elaborate soil moisture or water stress measuring devices may not be necessary if watering is carefully monitored. In field-grown trees water stress is difficult to control.

Cone buds have been induced in 6-year-old field-grown western hemlock seedlings in an experiment that used a combination of calcium or ammonium nitrate fertilizer (applied on May 26 at 42 g per plant), and foliar spray of $GA_{4/7}$, applied weekly for six weeks

[1]Available from Imperial Chemical Industries Ltd., U.K.

[2]Ibid.

[3]Available from Armak Co., Chicago, IL., U.S.A. 60690

[4]Steven Ross, personal communication, 1983, B.C. Ministry of Forests, Research Branch, Victoria.

starting on July 7. This treatment began late and, as a result, produced seed-cone buds, but no pollen-cone buds (Ross *et al.* 1981).

These methods give only rough guidelines to cone-induction techniques for western hemlock, and the original reports (Ross and Pharis 1981; Ross *et al.* 1981; Brix and Portlock 1982) should be consulted before treatments are attempted.

Experiments with mountain hemlock wild seedlings have been limited to foliar spray use of $GA_{4/7}$ (as above), and water stress, but no cones have been induced (authors' experiment).

Western hemlock offers considerable potential for cone production and rapid regeneration because of the relative ease with which cones can be induced, and the possibility that the sexuality of cones produced can be controlled to some extent by timing the treatments. Earlier treatments, during the natural time of pollen-cone bud differentiation (Fig. 16), may increase the proportion of pollen-cone buds, whereas later treatments, during the natural time of seed-cone bud differentiation (Fig. 16), may increase the proportion of seed-cone buds. Similar manipulation of cone sexuality may not be possible in mountain hemlock because pollen-cone and seed-cone buds differentiate at the same time under natural conditions (Fig. 17) (Owens 1984*b*).

Cone induction in young western hemlock could substantially shorten the long non-reproductive "juvenile" period that under natural conditions may take over 20 years. Cone induction will greatly facilitate hemlock tree improvement programs and could bring seed orchards into early productivity.

Identification of Buds

Dormant vegetative buds of western hemlock are pointed. The outer bud scales are thick, brown and pubescent, and the inner bud scales are thin and white (Owens and Molder 1973). Terminal buds are often obscured by several leaves. On vigorous shoots they are 3 to 5 mm long; on less vigorous shoots they are 2 to 3 mm long. Lateral buds are smaller and more narrow than terminal vegetative buds on the same shoot (Fig. 19). Vegetative terminal buds are enclosed by about 30 bud scales; lateral buds have fewer bud scales.

FIGURE 19. Dormant vegetative terminal and vegetative lateral buds of western hemlock. (X 4) LEFT

FIGURE 20. Dormant vegetative terminal bud of western hemlock after bud scales have been removed. (X 15) RIGHT

Dormant vegetative buds of mountain hemlock are broader, generally larger, and less pubescent than those of western hemlock (Figs. 25, 26). Otherwise, they are very similar in shape and colour. Vegetative terminal buds of mountain hemlock are enclosed by about 25 bud scales (Owens 1984*a*).

In both species the embryonic shoots within the buds are green, but vary in size and number of leaf primordia depending upon their vigour and position on the shoot. Large terminal and distal lateral buds contain many leaf primordia along a long shoot axis (Fig. 20), and the apical meristem is often visible at the tip. Less vigorous terminal and lateral buds contain few leaf primordia, and these are on a short shoot axis, with the shoot apex resting deeply between the leaf primordia (Fig. 12) (Owens and Molder 1973; Owens 1984*a*).

Dormant seed-cone buds of western and mountain hemlocks are similar in shape and colour. Those of mountain hemlock may be slightly larger. Seed-cone buds are approximately 3 mm long and are broader than vegetative buds from the same branches. Seed-cone buds have about 25 bud scales. The short, outer bud scales are light brown and pubescent. Several inner bud scales are dark brown, smooth and shiny, and form a conical tip over the bud. Inner bud scales are white and thin. The shoot at the base of the seed-cone bud of western hemlock usually bends at a distinct angle from the subtending shoot (Fig. 21). The shiny tip distinguishes most seed-cone buds of both species from vegetative buds. The embryonic seed cone within is green and appears similar in both species, except that those of mountain hemlock are slightly larger and have more bracts. At this stage, bracts are broad and leaf-like (Fig. 22), and ovuliferous scales are only tiny swellings at the base of the inner surface of most bracts. The apical meristem is completely covered by bracts (Owens and Molder 1974; Owens 1984*b*).

Dormant pollen-cone buds of western and mountain hemlocks are similar in size, shape, colour and position. Pollen-cone buds are approximately 2 mm long, and are oblong with a round tip (Figs. 23, 25). They have only about 10 bud scales. Outer bud scales are light brown and thick; inner bud scales are white and thinner. In western hemlock the inner bud scales or the dark green embryonic cone may show through the outer bud scales, giving the cone a light brown to green tip. The dormant pollen cones are round and berry-like (Figs. 24, 26). By dormancy all microsporophylls are formed. They have a rounded tip

FIGURE 21. Dormant seed-cone bud (SC) of western hemlock. (X 4) LEFT

FIGURE 22. Dormant seed cone of western hemlock after bud scales have been removed. (X 25) RIGHT

FIGURE 23. Dormant pollen-cone buds (PC) of western hemlock. The terminal bud has remained vegetative (VT) and a basal pollen cone (*) has developed from a latent bud on the previous year's shoot. (X 4) LEFT

FIGURE 24. Dormant pollen cone of western hemlock after bud scales have been removed, showing the rounded microsporangia. (X 30) RIGHT

and bear two large microsporangia. The cone apex is not visible (Fig. 24). The most distinctive feature of pollen-cone buds is their distribution; usually several such buds are clustered around the base of a short shoot (Figs. 23, 26) (Owens and Molder 1974; Owens 1984*b*).

FIGURE 25. Dormant pollen-cone (PC), seed-cone (SC) and vegetative (V) buds of mountain hemlock. (X 1.5)

FIGURE 26. Dormant pollen-cone (PC), seed-cone (SC) and vegetative (V) buds of mountain hemlock after some bud scales have been removed. (X 6)

Forecasting Cone Crops

It is often useful in the fall to estimate the abundance of cones that might be available for pollination in the spring and cone collection the next fall. In hemlocks this estimate can be made in August, although this requires tedious dissection of buds for identification. By September, bud identification is more reliable since buds do not change externally until spring.

Because the production of pollen cones and seed cones on a tree is usually closely correlated, it is easier to forecast the cone crop based on the more easily recognized pollen-cone buds. Sample branches collected from the middle, pollen-cone bearing portion of the crown can be sampled from several trees. The presence or absence of clusters of pollen-cone buds at the base of the short shoots (Fig. 23) can be determined quickly.

In any one location there are usually some trees bearing abundant cone buds — those individual trees that appear to have their own cycle of cone production, possibly modified by climate. Therefore, a sampling of trees in an area is necessary to provide an accurate forecast of potential cone crop. It should be emphasized that these bud counts can accurately forecast the absence of a cone crop, but not necessarily the abundance of a cone crop or seed crop. Frost, cone abortion, poor pollination, insects, and disease can seriously reduce a potential cone and seed crop between September, when cone buds can be recognized, and one year later when seeds are shed (Fig. 5) (Dobbs *et al.* 1976; Eis and Craigdallie 1981).

Pollen-Cone and Pollen Development

All microsporophylls are initiated rapidly during the first month of pollen-cone bud development (Fig. 5). Each microsporophyll then forms two "microsporangia" (pollen sacs) on its lower ("abaxial") surface. Microsporangia of dormant pollen-cone buds of both species contain many large, angular, loosely packed pollen mother cells ("PMC") (Figs. 27, 28*B*). Each microsporangium is lined with a single layer of cells,

FIGURE 27. Longitudinal section of a dormant pollen-cone bud showing microsporophylls (MS) and microsporangia (MSP) containing pollen mother cells (PMC). (X 60)

the "tapetum". The pollen mother cells begin "meiosis", a special form of cell division, in the fall. The chromosomes within each PMC duplicate, but the cells do not divide, and no further changes occur in the pollen cones before winter dormancy (Owens and Molder 1975).

Pollen-cone buds of coastal western hemlock resume growth in mid-February (Fig. 5) (Ho and Owens 1974); and in late March in mountain hemlock (Owens and Molder 1975). Pollen cones commonly change from green to purple and slowly enlarge, causing the buds to swell. There is then a brief period of rapid enlargement that causes the purple pollen cones to push through the bud scales at the tip of the bud. This rapid enlargement results initially from the development of pollen sacs as the PMC's complete meiosis and cell division. Each PMC forms four microspores, each with 12 chromosomes, half ("haploid") the original 24 (Fig. 28*C*). Meiosis is completed in late February in western hemlock (Ho and Owens 1974); and in mid-April in mountain hemlock (Owens and Molder 1975). Temperature may affect the time of meiosis in both species. Following the division process the microspores separate, each developing into a pollen grain (Figs. 28*D-H*).

Microspores are angular at first but later become round. A thick wall forms, consisting of two layers: a thick outer "exine" layer; and a thin inner "intine" layer.

Pollen development is quite different in the two species (Owens and Blake 1984). In western hemlock the pollen grain produces many long spines that extend from the roughly sculptured exine. The grain indents on one side but no wings develop (Fig. 29). In mountain hemlock the surface of the exine becomes finely sculptured. During the early development of mountain hemlock pollen the outer layer of the exine separates from the inner layer at two adjacent areas. The outer layer swells outward, forming two air-filled wings ("sacci") on the sunken, distal surface of the body ("corpus") of the pollen grain (Fig. 31). During

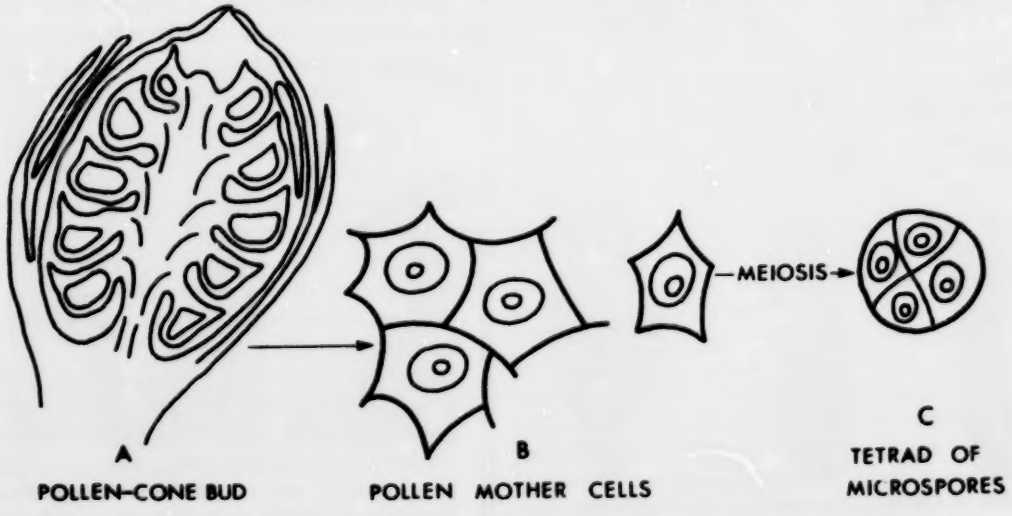


FIGURE 28. Pollen development of western hemlock after winter dormancy.

the later stages of pollen-wall development in both species the cells of the tapetum degenerate and some of their contents ("Ubisch bodies") are deposited on the surface of the exine.

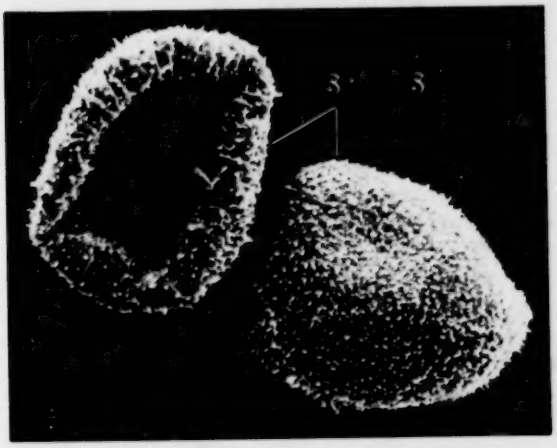


FIGURE 29. Scanning electron micrograph of mature, dry, western hemlock pollen. (X 630)

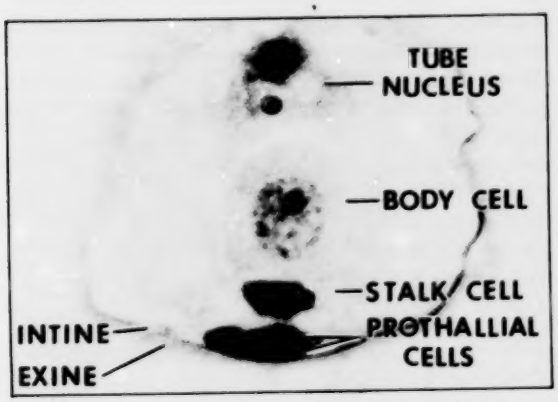


FIGURE 30. Section through mature imbibed western hemlock pollen. (X 900)

During pollen-wall development of both species, but after the sacci form in mountain hemlock, the single haploid microspore cell divides unequally twice, each time producing a small, lens-shaped "prothallial" cell on the proximal side of the pollen grain (Figs. 28*D*, 28*E*, 30, 32). The remaining large cell, or "antheridial initial", then divides unequally, producing a small "generative" cell and a large "tube" cell (Fig. 28*F*). The tube cell stores many starch grains. The generative cell divides equally, forming a "stalk" cell

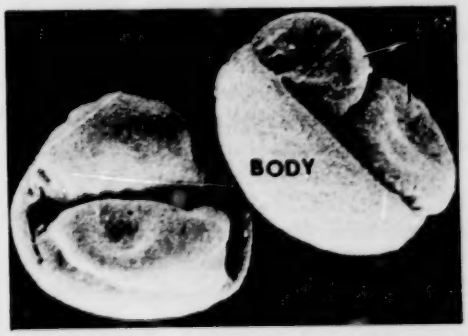


FIGURE 31. Scanning electron micrograph of mature, dry, mountain hemlock pollen. (X 700)

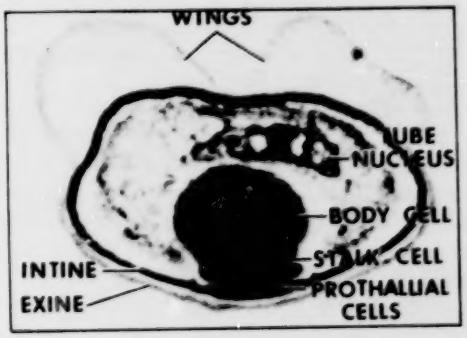
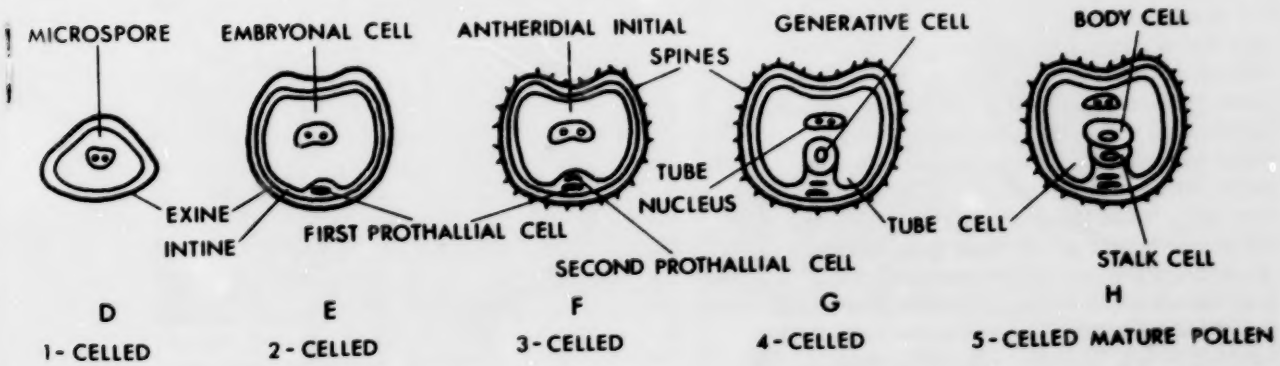


FIGURE 32. Section through mature imbibed mountain hemlock pollen. (X 1000)



adjacent to the prothallial cells, and a "body" cell. This forms the mature, five-celled pollen grain which is shed within a few days (Figs. 28*H*, 29-32). It is the body cell that eventually forms two male gametes after pollination (Ho and Owens 1974; Owens and Molder 1975).

The pollen grains of western hemlock are very distinct from those of mountain hemlock (Figs. 29, 31). This is unusual in most conifers, where pollen grains of species within a genus are often indistinguishable. Dry western hemlock pollen is spherical or bowl-shaped, without wings, and with an indentation at the distal pole. The average diameter of western hemlock pollen is 60 μ m (within a range of 59 to 71 μ m). The sculpturing is rough and warty in appearance, and many warts bear spines (Fig. 29). There are no morphological differences between pollen collected from coastal western hemlock and pollen collected from western hemlock growing in the interior of British Columbia. Dry mountain hemlock pollen is bowl-shaped, with two small wings separated by a deep furrow and set in a deep sinus on the proximal surface. Mountain hemlock pollen has a body length and width of approximately 60 μ m (within a range of 42 to 74 μ m). Sculpturing of the body is similar to, but finer than, that of western hemlock. Sculpturing on the wings is similar to that on the body, but the wings are somewhat smoother. No spines occur on the small warts (Fig. 31) (Owens and Simpson 1982).

During the last stages of pollen development the pollen-cone axis elongates, forming a long stalk that pushes the pollen cone out of the bud scales. The elongation of the cone axis separates the microsporophylls, and the pollen sacs split along a predetermined line of dehiscence where the wall is thin. Pollen cones are commonly pendant during pollination. A tree usually sheds the mature yellow pollen for about one week (Fig. 5). Dried, empty pollen cones may be retained on the tree for many months (Owens and Molder 1975; Owens and Blake 1984).

If quantities of good pollen are to be obtained, branches bearing pollen cones should be collected after the buds have emerged nearly fully from their bud scales. Unlike those of some conifers, hemlock pollen cones can be "forced" by placing the cut ends of the branches in water indoors. The later stages of pollen development will occur normally and viable pollen can be collected easily. Branches collected too early (at or before meiosis or during rapid swelling of pollen-cone buds) may not display normal pollen-cone development and may not produce viable pollen. If branches are not to be placed in water, they should not be collected more than a day or two before pollen shedding begins. Branches collected too early and left out of water may not shed any pollen, or may shed only immature pollen, which can be wet and clumped, with low viability. Cones collected after pollen shedding has begun may yield only small quantities of pollen.

Seed-Cone Bud Development

Seed-cone bud development in western hemlock occurs from about mid-July until the end of November (Fig. 16), during which time 30 to 40 bracts are initiated. In mountain hemlock, seed-cone bud development occurs from the end of July until mid-October (Fig. 17), and about 100 bracts are initiated. In both species, bracts at the base and tip of the seed cone do not develop ovuliferous scales. A few bracts toward the base and tip of the cone develop rudimentary ovuliferous scales that remain sterile (Fig. 33). The cone apical meristem in both species initiates a few small bracts after dormancy, but these seldom form ovuliferous scales and are sterile. Occasionally the seed-cone apical meristem of western hemlock will initiate a series of leaves after winter dormancy, forming a short vegetative shoot from the tip of the "proliferated" seed cone. The shoot dies in the fall when the cone dries and opens. In western hemlock two ovule primordia are initiated on the larger ovuliferous scales before dormancy. Within each ovule a single, large megaspore mother cell ("MMC") differentiates and is surrounded by layers of smaller cells of the megasporangium, or "nucellus" (Owens and Molder 1974). In mountain hemlock, ovules are not initiated until after winter dormancy (Owens 1984*b*).

FIGURE 33. Median longitudinal section of a dormant seed-cone bud from mountain hemlock showing the apical meristem (AM), bracts (B) and ovuliferous scales (OS). (X 30)

Seed-cone buds in coastal western hemlock resume growth in early February; in mountain hemlock this occurs in late March. The seed-cone buds enlarge within the bud scales, causing the buds to swell. The cone tips begin to push through the bud scales about three weeks before pollination begins (Owens and Blake 1984).

FIGURE 34. Scanning electron micrograph of a western hemlock bract and ovuliferous scale (OS) collected shortly after cone bud dormancy ended, showing two ovules, each with a nucellus (N) being overgrown by the integument tip (INT). (X 50)

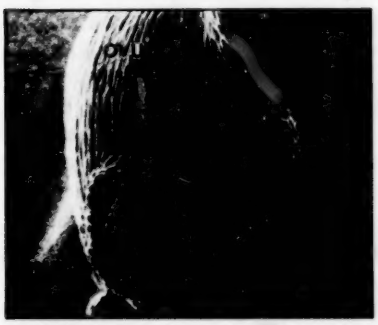


FIGURE 35. Scanning electron micrograph of a western hemlock ovule showing the nucellus (N) nearly covered by the funnel-shaped integument tip. (X 95)

During cone-bud enlargement a ring of tissue forms on the end of each ovule, adjacent to the cone axis (Fig. 34). This tissue elongates and forms the integument tip, which overgrows the "nucellus" (Fig. 35). In western hemlock, the integument tip develops into a short funnel with a wide opening ("micropyle") (Fig. 40). In mountain hemlock, the integument tip develops into two long, irregular flaps, with a small micropyle buried deeply between the flaps (Fig. 42). At pollination in both species, the integument tips extend beyond the ovuliferous scale into a space between the cone axis and adjacent ovuliferous scales (Owens and Blake 1984).

Pollination

The rate of pollen-cone and seed-cone development after dormancy is greatly affected by temperature. Development is rapid during warm weather but slows during cool or rainy weather. Consequently, there is much variation in the time of pollination according to different years and different areas. In western hemlock at low-elevation coastal British Columbia locations, pollination commonly occurs in early to mid-April (Ho and Owens 1974; Williamson 1976), whereas in the interior of British Columbia, it may occur from May until mid-June. Records from western Washington and Oregon show that pollination may occur from mid-April until late May (Fowells (compiler) 1965). Pollination in mountain hemlock at moderate elevations in coastal British Columbia occurs in mid-June (Owens and Molder 1975). There are reports, however, of pollination in mid-July at more northern and higher elevations (Fowells (compiler) 1965).

As the pollen-cone axis elongates and the cone emerges from the bud scales (Fig. 39), the microsporangia dry and split open to release the yellow pollen (Fig. 37). Pollen can be dispersed over

FIGURE 36. Western hemlock seed cone at pollination. The bract is light coloured and the ovuliferous scale (OS) is dark. (X 3) FAR LEFT

FIGURE 37. Western hemlock pollen cones (PC) at pollination. (X 4) LEFT

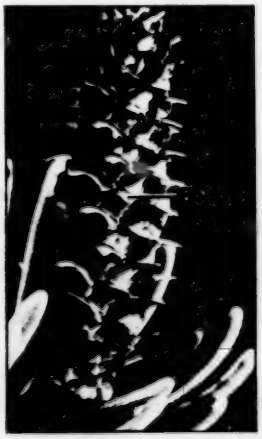


FIGURE 38. Mountain hemlock seed cone at pollination. Bracts are large, pointed and reflexed, obscuring the ovuliferous scale. (X 3) RIGHT

FIGURE 39. Mountain hemlock pollen cones (PC) just before pollen is shed. (X 1.5) FAR RIGHT

large areas by wind. As the seed-cone axis elongates, bracts separate and bend back, opening the spaces between the bracts and the small ovuliferous scales

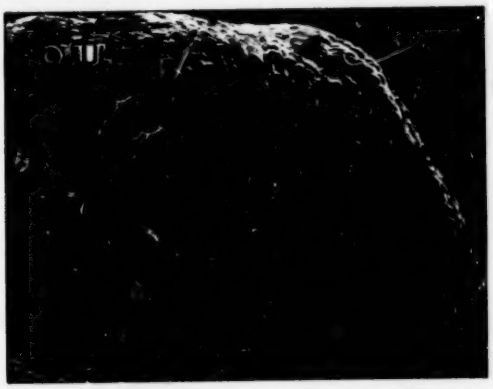


FIGURE 40. Scanning electron micrographs of a western hemlock ovule at pollination, showing pollen (P) in the open micropyle (M) and on the rim of the micropyle. (X 135)

FIGURE 41. Scanning electron micrograph of a western hemlock ovule after pollination, showing the nearly closed micropyle (M). (X 100)

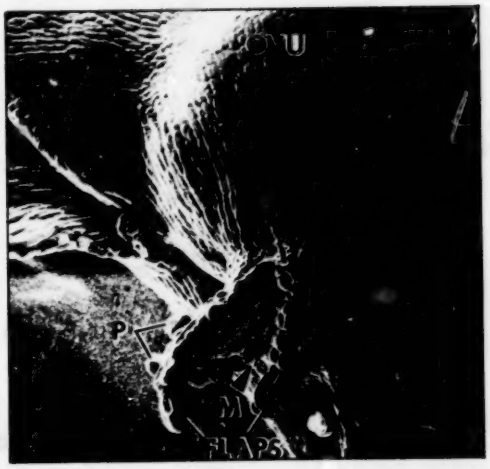


FIGURE 42. Scanning electron micrograph of a mountain hemlock ovule at pollination, showing the micropyle (M) and two micropylar flaps with pollen (P) adhering. (X 70)

(Figs. 36, 38) to expose the ovules. This allows pollen to sift between the bracts and scales. Seed cones are open and receptive for one to two weeks in both species (Owens and Blake 1984).

Western hemlock seed cones are usually purple and remain horizontal or pendant during pollination (Fig. 36). Pollen adheres to the bract, ovuliferous scale, or ovule, and some may enter the micropyle or adhere to the edge of the funnel-like integument tip (Fig. 40). After five to six weeks, pollen germinates on almost any surface within the cone. Each pollen grain forms a long, thin pollen tube that grows over the surface to the micropyle — or simply from the funnel rim into the micropyle. Several pollen tubes may grow down the micropylar canal to each nucellus. After about two to three weeks the ovuliferous scales enlarge rapidly, thicken, and seal the cone (Owens and Blake 1984). The funnel may later "crimp in" and the micropyle becomes nearly sealed (Fig. 41).

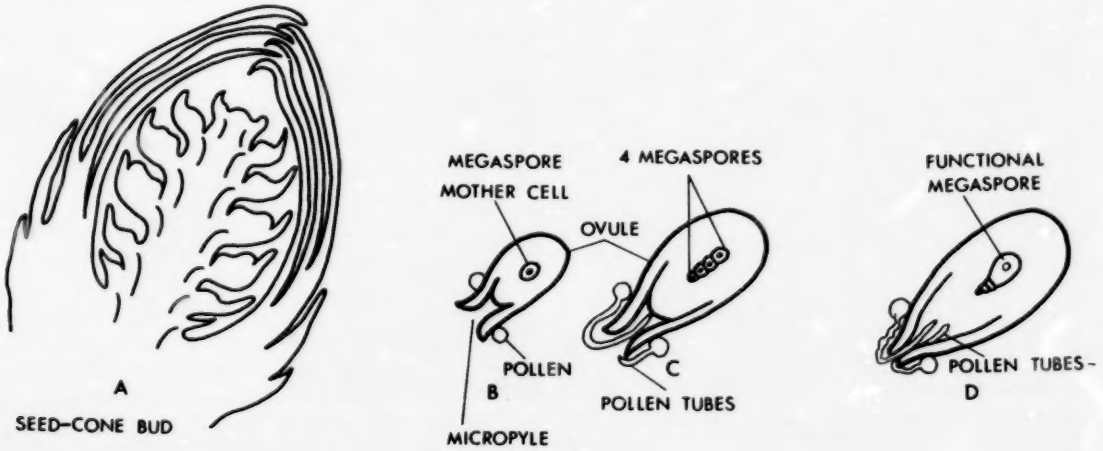


FIGURE 47. Female gametophyte development in western and mountain hemlocks.

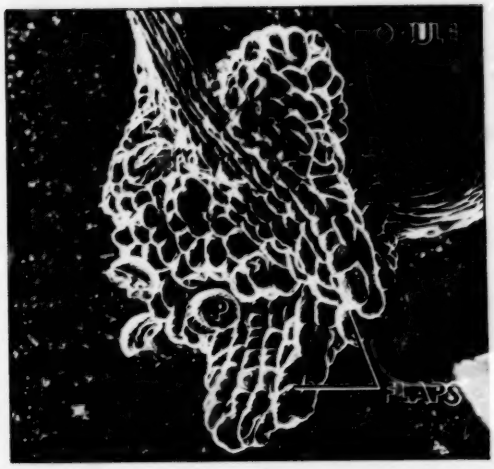


FIGURE 43. Scanning electron micrograph of a mountain hemlock ovule after pollination, showing the collapsed micropylar flaps with pollen (P) adhering. (X 100)

Mountain hemlock seed cones are purple to green and usually erect during pollination (Fig. 38). Cells on the two flaps of the integument tip secrete sticky microscopic droplets. Although pollen may adhere to all surfaces of the seed cone, many pollen grains adhere to the inner surface or edge of the splayed sticky flaps (Fig. 42). Within about one week, the flaps come together and adhere loosely along their sticky surfaces, usually entrapping several pollen grains (Fig. 43) (Owens and Blake 1984). The pollen entrapped between the flaps then germinates and grows down the micropylar canal. The nucellus also begins to elongate down the micropylar canal. Pollen adhering to bracts and ovuliferous scales does not form long pollen tubes that grow into the micropyle, as they do in western hemlock. After seed cones have been receptive for about one week, the ovuliferous scales enlarge, thicken, and seal the cone. Seed cones remain nearly erect on the twigs until late July, when the weight of the seed cone causes the twig to bend downward and the cones to become pendant (Fig. 2) (Owens and Molder 1975).

Ovule Development

Soon after winter dormancy ends in western hemlock (but not until the ovule has formed during the spring in mountain hemlock), the MMC in each ovule (Figs. 44, 47*B*) enlarges, and then undergoes meiosis. Meiosis of the MMC occurs during early March in western hemlock, and during late May in mountain hemlock. Despite the considerable difference in phenology between the two species, development is the same. Meiosis produces four megaspores, each with half the original 24 chromosomes. The megaspores form a linear tetrad (Figs. 45, 47*C*), and the middle two megaspores are not separated by a cell wall. The three outer megaspores degenerate and the inner, functional megaspore (Figs. 46, 47*D*) develops into the female gametophyte (Fig. 47). Development of the female gametophyte takes about three months in western hemlock (Staniske and Owens 1974), and about two-and-a-half months in mountain hemlock (Owens and Molder 1975).

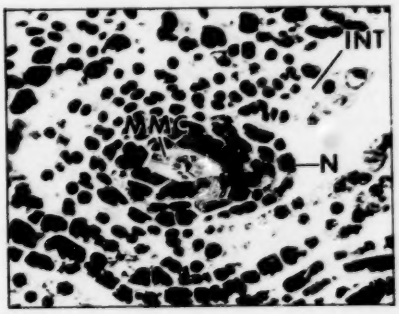
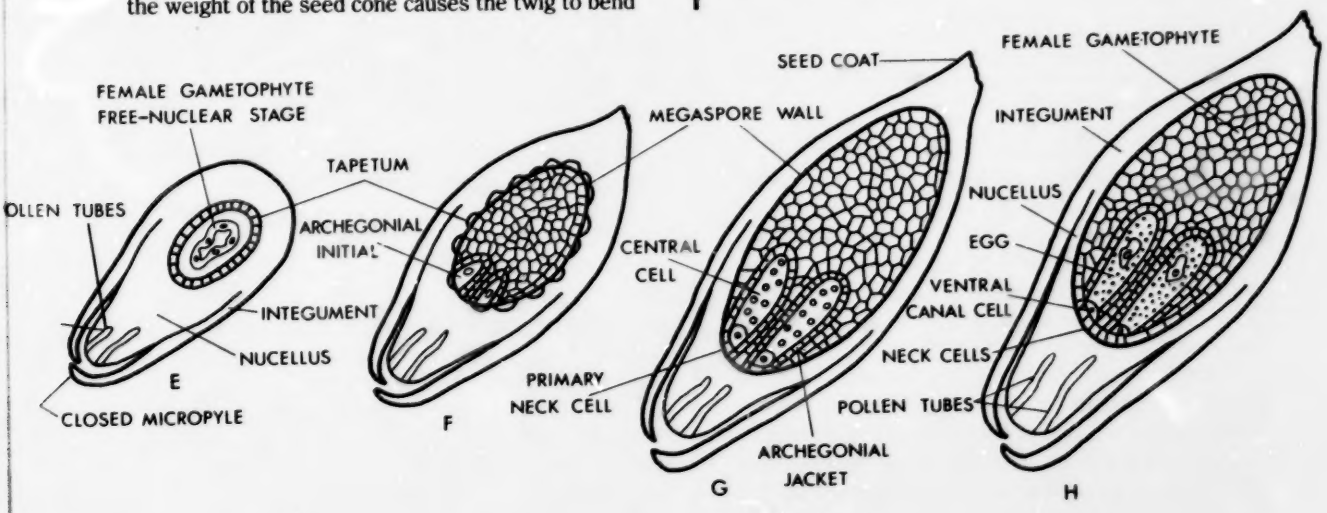


FIGURE 44. Longitudinal section of an ovule showing one large megaspore mother cell (MMC) in the nucellus (N), all within the integument (INT). (X 250)



The functional megaspore enlarges, forms many large vacuoles (Fig. 46), and begins a series of free nuclear divisions. An irregular, sac-like free nuclear female gametophyte forms, consisting of a thin parietal layer of multinucleate cytoplasm around a large central vacuole (Fig. 47*E*). The female gametophyte is bounded by a megaspore wall that later thickens (Figs. 47*F, G*) and becomes sculptured, much like the wall of the pollen grain. Outside the megaspore wall is a spongy tapetum, which degenerates during female gametophytic development (Figs. 47*F, G*), adding to the thickness and sculpturing on the surface of the megaspore wall.

The sac-like free nuclear female gametophyte (Fig. 47*E*) enlarges, and then displays rapid cell-wall formation, producing a female gametophyte of many

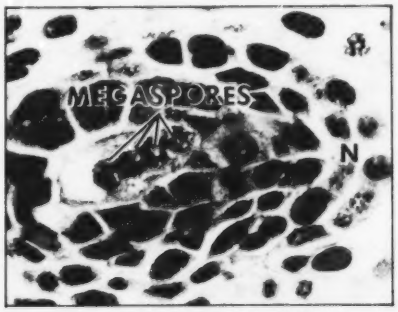


FIGURE 45. Longitudinal section of a nucellus (N) containing a linear tetrad of megaspores. (X 470)

FIGURE 46. Longitudinal section of a nucellus (N) containing the enlarged, vacuolate, functional megaspore (FM) and the three degenerated megaspores (DM). (X 370)

large uninucleate cells. Most of these cells divide to form many smaller cells. However, at the micropylar end of the female gametophyte several cells do not divide, but enlarge and function as archegonial initials (Figs. 47*F*, 48). Several small cells remain around the archegonial initials. These cells form a single layer of archegonial jacket cells that enclose each archegonial initial except at the micropylar end.

Each archegonial initial enlarges, becomes vacuolate, and then divides unequally, producing a small primary neck cell at the micropylar end and a large central cell (Figs. 47*G*, 49). In western hemlock each primary neck cell divides to form one or two layers of several neck cells per layer.

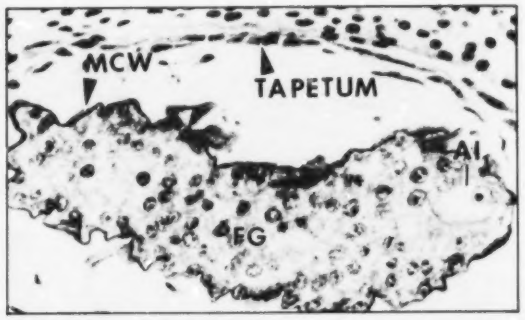


FIGURE 48. Longitudinal section of a cellular female gametophyte (FG) inside the megaspore cell wall (MCW), showing one of the archegonial initials (AI). (X 200)

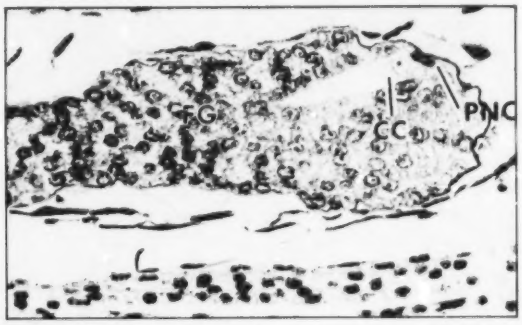


FIGURE 49. Longitudinal section of a female gametophyte (FG) showing the large central cell (CC) and the primary neck cell (PNC) of the archegonium. (X 200)

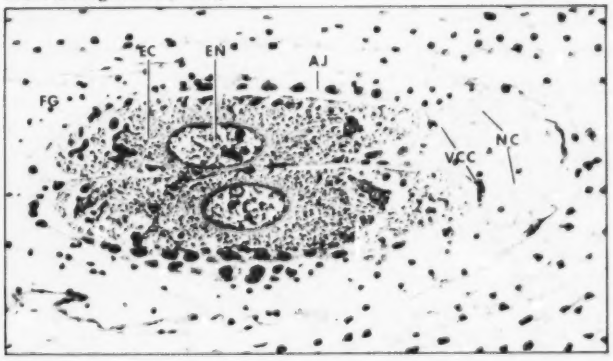


FIGURE 50. Longitudinal section of an ovule, showing part of the mature female gametophyte (FG) containing two archegonia, each consisting of an archegonial jacket (AJ), ventral canal cell (VCC), neck cells (NC), egg nucleus (EN) and egg cytoplasm (EC). (X 200)

Many large vacuoles form in the central cell, giving it a frothy appearance (Fig. 47*G*). The vacuoles become filled with large and small inclusions, often called "proteid bodies". During this process the central cell divides unequally, forming a small ventral canal cell, adjacent to the neck cells, and a large egg cell. When the egg cell nucleus migrates to the centre of the egg, the female gametophyte is mature and ready for fertilization (Figs. 47*H*, 50).

Female gametophytes of western hemlock contain two to five archegonia, and those of mountain hemlock, two to four archegonia. The number of archegonia, and thus the number of eggs that can be fertilized in these two species, is about the same as in many other

members of the Pinaceae (Stanlake and Owens 1974; Owens and Molder 1975; Singh 1978).

The female gametophyte is mature approximately six weeks after pollination. This is typically during mid-May in coastal western hemlock (Fig. 5), and late July in mountain hemlock. During female gametophyte development, the ovules and seed cones enlarge to their mature size and store abundant food reserves. Seed wings develop from the ovuliferous scales, and cones of both species become heavy, pendant, and red to purple. During later stages of female gametophyte development, ovules become hard as the seed coat differentiates from the integument. At this stage the eggs within the ovules are ready to be fertilized (Stanlake and Owens 1974; Owens and Molder 1975).

Fertilization

Several pollen tubes may grow into the nucellus, but no more than one pollen tube penetrates each archegonium (Fig. 51*A*). As the pollen tubes grow through the nucellus, the body cell, which is carried along in the pollen tube, divides to form two male gametes, one larger than the other (Fig. 52). The pollen tube grows through the neck cells (Fig. 52) and the ventral canal cell, all of which appear to be destroyed by this process. The contents of the pollen tube are then released into the egg cell (Fig. 51*A*). A receptive vacuole results from the discharge of the pollen tube contents into the egg cytoplasm (Fig. 53).

The two male gametes lack any visible means of movement, but despite this, the larger male gamete moves through the egg cytoplasm and fuses with the egg nucleus. This constitutes fertilization. The smaller male gamete and other contents of the pollen tube degenerate. Fertilization occurs in coastal western hemlock about mid-May (Fig. 5), and in mountain hemlock in early August. All eggs within an ovule may not be fertilized. Unfertilized eggs degenerate within one to two weeks. If adequate viable pollen is present, at least one egg within the female gametophyte is usually fertilized. Although pollen or pollen tubes need not be present for female gametophytes, ovules, and cones to develop, if no eggs are fertilized within a female gametophyte, it will degenerate, leaving a normal-appearing but empty seed (Stanlake and Owens 1974; Owens and Molder 1975).

Embryo Development

As in other conifers, embryo development in hemlocks can be separated into two phases: the short, proembryo phase that occurs within the archegonium (Figs. *A-H*); and the longer embryo phase, that occurs after the proembryo has grown out of the archegonium and into the female gametophyte tissue (Figs. 51*E-F*) (Foster and Gifford 1974; Singh 1978).

Proembryo development begins when the fertilized egg nucleus divides first into two (Fig. 51*A*), and then four free nuclei, all contained within a dense region of neocytoplasm in the centre of the egg cell (Fig. 53). The neocytoplasm and the four free nuclei then migrate to the end of the egg cell opposite the neck cells. The nuclei become oriented into a single tier (Fig. 51*B*). Each nucleus divides and cell walls develop between the eight nuclei to form two tiers of four cells each (Figs. 51*C*, 54). The four cells in each tier divide again, forming a 16-celled proembryo consisting of four tiers of four cells each (Figs. 51*D*, 55). The proximal "open tier" remains receptive to the egg cytoplasm and apparently functions to absorb nutrients stored in the egg cytoplasm. The adjacent "rosette tier" has no known function, but in some conifers may divide and form small clumps of cells — often mistakenly called "rosette embryos". These cells soon degenerate. The next tier of cells, the "suspensor tier", elongates and pushes the distal "apical tier" through the archegonial jacket and into the female gametophyte tissue (Fig. 51*E*). This ends the proembryo stage, which lasts about one week in both species, and begins the "early embryo" stage (Figs. 51*E-H*) (Stanlake and Owens 1974; Owens and Molder 1975).

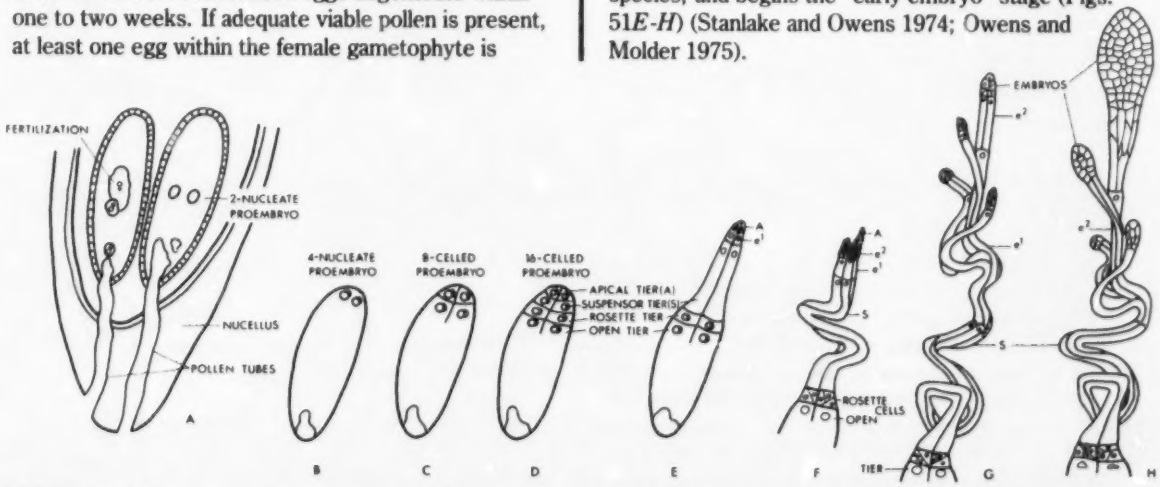


FIGURE 51. Fertilization and embryo development in hemlock. (A) apical cells; (e^1), (e^2) embryonal tubes; (S) suspensor.

FIGURE 52. Longitudinal section of an ovule just before fertilization, showing an archegonium (A) and a pollen tube (PT) containing two male gametes (MG). (X 175) FAR LEFT

FIGURE 53. Longitudinal section of an ovule just after fertilization, showing the four free nuclei (FN) of the proembryo and the receptive vacuole (RV) inside the archegonium. (X 200) LEFT

FIGURE 54. Longitudinal section of an ovule showing a two-tiered, eight-celled proembryo (PE). (X 280) RIGHT

FIGURE 55. Longitudinal section of an ovule showing a 16-celled proembryo, consisting of an apical tier (AT), suspensor tier (ST), rosette tier (RT) and open tier (OT). (X 270) FAR RIGHT

Cells of the apical tier divide to form distal, apical cells and basal, embryonal tubes. Embryonal tubes elongate and force the apical cells further into the female gametophyte (Fig. 51*F*).

Hemlocks, like most conifers, undergo two types of "polyembryony", the process by which several embryos may develop within one ovule (Foster and Gifford 1974; Singh 1978). "Simple polyembryony" occurs when more than one egg is fertilized within an ovule (Fig. 51*A*). Western and mountain hemlocks average about three eggs (each one within an archegonium) per ovule and commonly more than one egg is fertilized. Each resulting proembryo could develop into a mature embryo. In simple polyembryony, each embryo is a result of fertilization by gametes from separate pollen grains (Fig. 51*A*) and, therefore, proembryos are genetically different. One proembryo usually is more vigorous and outgrows the others, which then degenerate.

The second type of polyembryony, "cleavage polyembryony", occurs after the suspensor tier elongates and cells of the apical tier divide to form the embryonal tubes (Fig. 51*E*). Cleavage refers to the separation of the apical cells into four files of cells (Fig. 51*F*), each of which can develop into a separate but genetically identical embryo (Fig. 56) (Owens and Molder 1973; Foster and Gifford 1974). As with simple polyembryony, usually one of the embryos resulting from cleavage is more vigorous and outgrows the others, which soon degenerate (Figs. 51*G, H*). In

FIGURE 56. Longitudinal section of an ovule showing four early embryos developing in the corrosion cavity (CC) formed by the collapse of female gametophyte cells (FG). (X 140) LEFT

FIGURE 57. Longitudinal section of an ovule containing one surviving, club-shaped embryo in the corrosion cavity (CC). Darkly staining storage products are accumulating in the female gametophyte (FG). (X 110) CENTRE

FIGURE 58. Longitudinal section of an ovule containing one young embryo, and showing the location of cotyledon (C) initiation, shoot apical meristem (SA), root apical meristem (RA), and secondary suspensor (S). (X 120) RIGHT

a hemlock ovule having four eggs, all of which become fertilized, four proembryos could form by simple polyembryony (Fig. 56). In turn, each proembryo could form four embryos by cleavage polyembryony. Consequently, 16 young embryos may begin to develop, though a mature seed seldom has more than one mature embryo. Usually, all other embryos stop development at a very early stage, degenerate, and are reabsorbed.

Each apical cell at the tip of the embryonal tube cells (Fig. 51*E*) divides many times (Fig. 51*F*), and forms a small multicellular embryo at the tip of a coiled suspensor (Figs. 51*G*, 56). All but one of the small embryos usually then degenerate (Figs. 51*G*, *H*). The remaining club-shaped embryo that survives (Fig. 57) is pushed to the middle of the female gametophyte by the coiled suspensor cells and embryonal tubes (Fig. 51*H*). Here the embryo enlarges rapidly. Cells at the distal end form several "cotyledons" or embryonic leaves, around a small shoot apical meristem. The root apical meristem forms in the central portion of the embryo. The more basal cells form a thick secondary suspensor (Fig. 58). This stage of development is reached by western hemlock embryos in early July (Stanlake and Owens 1974), and by mountain hemlock embryos in late August (Owens and Molder 1975). The embryos of western and mountain hemlocks then go through a six-week period of embryo growth before embryos are mature. During this time the "hypocotyl" or embryonic shoot, and cotyledons elongate, and provascular tissue appears. A massive root cap develops from the root apical meristem, but the shoot apical meristem remains small and inactive (Fig. 59) (Stanlake and Owens 1974; Owens and Molder 1975).

As the embryo extends into the female gametophyte, stored food is dissolved and a region of clear cells is left around the embryo (Figs. 56-58). These female gametophyte cells degenerate, forming a corrosion cavity in which the embryo develops. The remaining female gametophyte cells contain storage products (Figs. 56-58) in the form of starch and lipo-protein, which are utilized during seed germination (Foster and Gifford 1974; Singh 1978).

FIGURE 59. Longitudinal section of a mature mountain hemlock seed with the seed coat removed, showing the darkly staining female gametophyte (FG) and the embryo, consisting of cotyledons (C), shoot apical meristem (SA), hypocotyl (H), root apical meristem (RA) and root cap (RC). (X 32)

Seed Development

The seed coat (testa) begins to differentiate from the integument before fertilization. The integument forms into three distinct layers: (1) an outer layer ("sarcotesta") that is thin and dark, and fused with the seed wing; (2) a hard middle layer ("sclerotesta") of thick-walled cells; and (3) a thin inner layer ("endotesta") (Singh 1978). A nearly continuous layer of nucellar tissue lies inside the seed coat and loosely envelopes the female gametophyte. A very thin, grey megaspore cell wall is firmly attached to, and encloses, the female gametophyte (Fig. 60).

FIGURE 60. Section through part of a mature seed. Shown is the seed coat, consisting of an outer (OL), middle (ML) and inner layer (IL). Inside the seed coat are the nucellus (N), megaspore cell wall (MCW) and the female gametophyte (FG). (X 370)

A seed wing develops from the ovuliferous scale on the end of the seed opposite the micropyle (Figs. 63, 64). The seed wing begins to develop at pollination and by the time of fertilization, a distinct seed wing two to three cells thick has formed. A separation layer develops beneath the ovule and seed wing during early embryo development. Complete separation of seed and seed wing from the ovuliferous scale occurs before the embryo is mature (Stanlake and Owens 1974; Owens and Molder 1975).

In the mature seed the embryo is loosely packed within the rather firm, white, nutritive female gametophyte tissue, often called "endosperm" (Figs. 59, 61). Coastal western hemlock seed is usually mature in September, about five months after pollination (Stanlake and Owens 1974). Cones begin to shed seed in September. Seeds appear mature in

mountain hemlock by about mid-September, but some changes in food reserves in the embryo and female gametophyte may occur until mid-October, when seed shedding may begin.

Cone Maturation, Seed Release, and Regeneration

Seed cones of both species are commonly red to purple during development, but turn brown in the fall as they dry and begin to open. Cones of both species open as a result of drying, which causes the cone scales to separate and reflex. The time from pollination to seed release ranges from 120 to 160 days in western hemlock (Edwards 1976), and 90 to 120 days in mountain hemlock (Owens and Molder 1975), and is a criterion for judging seed maturity. These times, however, are only estimates, and can vary according to weather and temperature during cone maturation. Dry, warm weather in late summer may cause more rapid drying and earlier opening of cones with, consequently, earlier seed release. Wet, cool weather at that time may delay cone opening and seed release.

Most seeds are shed in the fall when cones first open. Cones may close in wet weather and reopen more fully with subsequent dry weather. This may happen many times, and as a result, seeds may be shed throughout the winter or even during the next spring (Edwards 1976). Mature cones often persist on the tree throughout the second year, but contain few viable seed. Western hemlock usually retains mature cones longer than does mountain hemlock.

Western hemlock cones have 20 to 30 scales, but those at the base and tip of the cone are usually sterile. Often less than 40 full-sized seeds per cone are produced, of which less than 20 are filled (Edwards 1976). Mountain hemlock cones have 80 to 100 scales, with some sterile scales at the base and tip (Meagher 1976). About 70 full-sized seeds are produced per cone, of which an average of 30 may be filled (Owens and Molder 1975). These estimates of filled seed per cone are based on open-pollinated cones, where considerable variation can occur. In some years there may be few or no filled seeds per cone. The amount and proporation of filled seed per cone may be increased greatly through the use of controlled pollinations. The number of fertile cone scales per cone multiplied by two (the number of ovules per scale) gives an estimate of the potential seed set, or seed potential, that could be obtained under optimal conditions.

Ovules at the base and tip of the cone either do not develop, or develop more slowly than ovules from the central portion. Ovules in the cone's extremities, whose development is slowed or arrested, remain as small, flat seeds. These contain no female gametophyte, and may have small wings. Ovules from the central, fertile portion of the cone may also abort during early development, forming flat seeds (Fig. 63). Ovules that are not pollinated form normal looking, but empty seeds (Figs. 63, 64). This occurs because pollen is not required for normal female gametophyte, ovule, or cone development. Empty seeds contain no embryo, only a shrivelled female gametophyte (Fig. 62) that aborted after the time when fertilization normally would have occurred. Filled, but inviable seeds usually result from incomplete embryo development or seeds damaged after maturation. Normal viable, filled seeds contain well-developed embryos (Stanlake and Owens 1974; Owens and Molder 1975; Hedlin *et al.* 1980).

FIGURE 61. Mature, filled western hemlock seed that has been sliced with a sharp razor blade, showing the seed coat (SC), female gametophyte (FG) and embryo (E). (X 20) LEFT

FIGURE 62. Mature, empty western hemlock seed that has been sliced with a sharp razor blade to show the brown, shrivelled female gametophyte (FG) without an embryo. (X 20) RIGHT

Seeds are small in both species. Western hemlock seeds are smaller (Fig. 63), ranging from 371 000 to 900 000 cleaned seeds/kg, averaging 530 000. Mountain hemlock seeds (Fig. 64) range from 346 000 to 477 000 cleaned seeds/kg, averaging 405 000 (Ruth 1974; Dobbs *et al.* 1976; Meagher 1976).

The seed wings of both species are large (Figs. 63, 64), enabling seeds to be distributed over great distances. In western hemlock most seeds fall within about 600 m of the base of tall trees growing in open, moderately windy areas. Some seeds can travel as far as 1150 m under these conditions. In a dense stand,

however, most seeds fall much closer to the base of the tree (Fowells (compiler) 1965). Comparable information is not available for mountain hemlock but the heavier seeds, and the consequent faster rate of fall, would result in less extensive seed distribution. Little is known about insect, disease, or animal destruction of dispersed seeds, but usually only a small percentage of the produced seeds germinate (Fowells (compiler) 1965).

FIGURE 63. Mature western hemlock seeds. Upper surface of a filled seed is on the left and the lower surface of a flat, empty seed is on the right. (X 8)

FIGURE 64. Mature, filled mountain hemlock seeds showing upper surface on the left and lower surface on the right. (X 8)

Coastal western hemlock is a prolific seed producer. Seed is produced by some trees every year and heavy seed crops occur every three to four years (Fowells (compiler) 1965). Even trees in dense stands can produce heavy cone crops. Interior western hemlock, as well, produces frequent heavy cone crops (Fowells (compiler) 1965). Less is known about the frequency of cone crops and the amount of seeds produced by mountain hemlock. Although it is considered to be a prolific seed producer, bearing some seeds almost every year (Fowells (compiler) 1965), cone crops occur less often than in western hemlock. Mountain hemlock cones are generally restricted to upper regions of the crown and are rarely as abundant as on western hemlock (Owens and Molder 1974; Owens 1984*b*).

In favourable climates western hemlock seeds can germinate soon after being shed, apparently having no prechilling requirement (Edwards 1976). If adequate moisture is available, germination under forest conditions is excellent on very diverse seed beds such as mineral soil, humus, decaying litter, moss, decaying logs, and stumps. Seedlings are exceptionally shade tolerant but very sensitive to heat, cold, drought, and wind (Kuser and Ching 1980). The small seeds result in a weak tap root system and this, coupled with rather delicate foliage, make western hemlock sensitive to dessication (Haddock 1976). Its shade tolerance, however, allows it to become established readily on the forest floor, where it may thrive in contrast to less shade tolerant conifers. Height growth of seedlings is usually slow during establishment, but thereafter, western hemlock may grow rapidly (Fowells (compiler) 1965; Williamson 1976).

Most mountain hemlock seeds are shed in the fall. Since this species commonly grows where there is snow cover during winter, apparently the seeds require prechilling. Most germinate in the spring, with germination occurring on either mineral or organic soil if sufficient moisture is present. Seedlings grow best in partial shade and develop slowly. Seedlings of mountain hemlock are less shade tolerant and more resistant to temperature and moisture extremes than those of western hemlock. Consequently, mountain hemlock commonly invades open areas at high elevations, but is slow to invade recently disturbed areas (Fowells (compiler) 1965).

Cone Collection and Seed Extraction

The proper time for cone collection is important and varies with the species being collected, the site, and the year. It is recommended that a sample of cones be collected from several trees in an area and that these cones be cut longitudinally to determine the number of filled seeds per half-section of cone. This provides information on the number of filled seeds per cone and helps determine if the cone crop is worth collecting. If sufficient cones and filled seeds are present to warrant a collection, samples of cones should be taken periodically to assess seed maturity and establish collection time. Seed maturity can be estimated by

seed cutting tests, where individual seeds are removed from cones, sliced longitudinally (Figs. 61, 62), and examined. Seed maturity can be estimated by the percent elongation of the embryo (Dobbs *et al.* 1976) and the appearance of the cones.

Because seeds can mature as early as August, sampling of cones should begin then. Mature embryos fill about 80% of the embryo cavity in the female gametophyte tissue (Fig 61). However, many changes occur in the seeds after the embryo is fully elongated. As seed cones ripen they turn yellow-brown and the scales start to dry and separate. Allen (1958) recommends mid-September as a suitable date to begin collecting cones, but in some dry, warm areas seeds may have begun to fall by this time.

Western hemlock cones are small (Fig. 1) and difficult to harvest. They can also be retained on the tree for more than a year. Consequently, last year's cones can be collected with the current year's cones. Old cones are dark brown, and although they open widely with little drying, they seldom contain filled seed.

The larger mountain hemlock cones (Fig. 2) are usually restricted to upper regions of the crown, making them difficult to collect. Because mountain hemlock seeds do not usually mature until October (Owens and Molder 1975), cone sampling should begin in September. Mature embryos fill about 90% of the seed (Fig. 59). Less is known about cone collection and handling for mountain hemlock than for western hemlock (Dobbs *et al.* 1976; Edwards 1976).

Hemlock cones collected in the field can be stored in permeable bags for various lengths of time prior to seed extraction, depending upon the maturity of the cones when collected. For western hemlock the recommended procedure is to delay cone collection as long as possible, and to store cones for as short as possible (Edwards 1976). Because of the high moisture content of many western hemlock cones when they are collected, their seeds are generally extracted promptly after picking. If they are too moist and stored for too long, seeds can become moldy or they can germinate within the cones. However, under proper storage for two months, western hemlock seed may not be harmed and seed quality of some seed lots may even be improved. Storage is best in a cool, well-ventilated area where cones can be spread in a thin, even layer. Although comparable information is not available for mountain hemlock, they appear to be amenable to storage for at least as long as western hemlock.

The temperature currently used in the kiln to open hemlock cones for seed extraction is 41°C for 18 to 20 hours[1]. Cleaning of seeds and removal of seed wings must be done carefully so that the thin seed coat is not damaged. Any damage to the seed coat can greatly reduce the storage life and viability of the seed. The small size of hemlock seed means that many light, but filled, seeds are lost during the cleaning process. These seeds, however, are frequently of lower quality than other seeds and the cost to sort these seeds from empty seeds may not be worthwhile (Edwards 1976).

[1 and 2]British Columbia Ministry of Forests, Seed Centre, personal communication, 1982, Duncan, B.C.

Seed Storage and Germination

Dry, undamaged hemlock seeds (Fig. 65), having a moisture content of 5%, store well for many years in closed plastic bags at -20°C, without a significant decrease in viability. Western hemlock seeds are not deeply dormant and many seed lots germinate readily without any presowing treatment. However, more uniform and, usually, more rapid germination occurs if seeds are placed in cool, moist conditions ("stratification") before sowing (Duffield 1950). Current stratification for western and mountain hemlocks involves placing seeds, which have been soaked in water for 24 hours, at 2°C for 28 days before sowing. Germination tests are made at 20°C for 28 days under eight hours of light[2]. Western hemlock seeds are very sensitive to incubation temperature: germinative rate is approximately halved for each 5°C-decrease in temperature. Also, germination is slower under light periods that last longer than eight hours (Edwards 1976). Studies for mountain hemlock seeds are not as complete as for western hemlock seeds and consequently, procedures adopted for mountain hemlock in the future may differ.

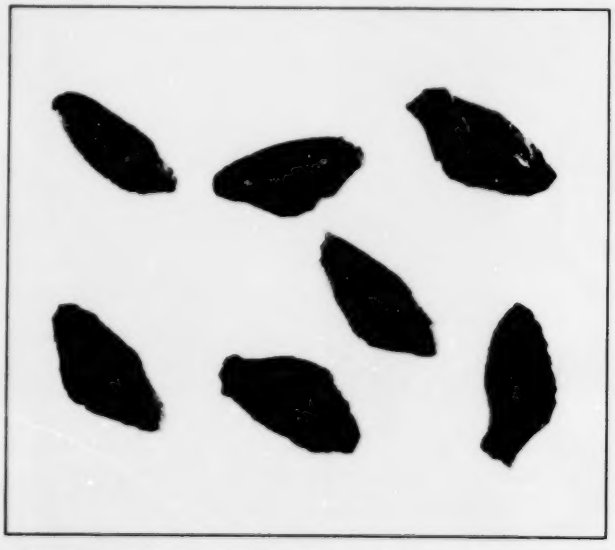


FIGURE 65. Dewinged western hemlock seed. (X 5)

The Seedling

Seed germination occurs when the embryonic root ("radicle") and embryonic shoot ("hypocotyl") (Fig. 59) elongate and force the root out of the micropylar end of the seed. Next, cotyledons and hypocotyl elongate and force the germinant from the seed coat. The seed coat usually adheres to the tips of the cotyledons for a short time (Fig. 66) before being shed. Embryos have three to six cotyledons (Ruth 1974).

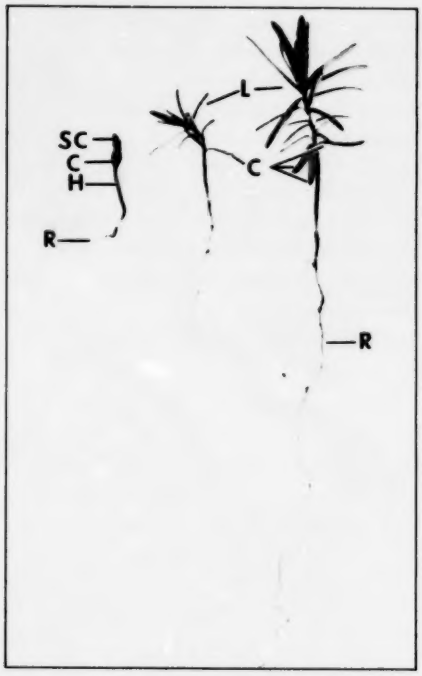


FIGURE 66. Western hemlock seedling development, showing the seed coat (SC), cotyledons (C), hypocotyl (H), primary root (R) and leaves (L). (X 1.5)

The small apical meristem located at the tip of the stem, just above the cotyledons, initiates new stem tissue and a spiral of leaf primordia that develop immediately, representing the first free growth period. The stem and primary root elongate (Fig. 66) throughout most of the growing season. Lateral branch apical meristems can be initiated in the axils of some of the leaves. These lateral branches form several leaves (Fig. 67). Lateral branch roots form from the primary tap root and these branch in turn, usually forming an extensive root system (Fig. 67).

When seedling growth slows late in the summer, the apical meristems of the terminal and lateral shoots form a series of brown bud scales, followed by a spiral of leaf primordia on the embryonic shoot. The bud scales enclose the embryonic shoot and leaf primordia, and these structures constitute the vegetative bud, which will resume growth, flush, and elongate after winter dormancy.

FIGURE 67. Container-grown 1-year-old (1-0) mountain hemlock (left) and western hemlock (right) seedlings. (X 75)

The period of free growth in the seedling occurs when leaf primordia and stem tissue elongate immediately after being initiated. It occurs in all conifer seedlings during the first year's growth. The end of free growth and the beginning of the formation of a winter bud is caused by a shortening of the day length (or increase in night length). Mountain hemlock seedlings begin to form a bud in mid-summer, whereas western hemlock seedlings can continue free growth until September. Seedlings can have a period of free growth in the spring for several years. In mature western hemlock a brief period of free growth may occur after winter dormancy in leader shoots and in vigorous lateral shoots. With the formation of terminal and axillary buds in the fall of the first growing season, the pattern of vegetative bud and shoot development becomes established. In subsequent years, vegetative buds normally pass through the same predictable cycle of winter dormancy, bud scale initiation, leaf initiation, and, once again, winter dormancy (as has been described for vegetative buds of mature trees).

Summary

Western and mountain hemlocks represent two sections of the genus *Tsuga*. Mountain hemlock is the only North American member of a once more widely distributed section of hemlocks. Western hemlock is

very similar morphologically to most other living hemlocks.

The reproductive cycles of western and mountain hemlock are essentially the same, but they can display variation in the phenology of reproductive development at different latitudes or different elevations. The reproductive cycles of both species extend over 15 to 16 months from the time of cone initiation in early summer, until seeds are shed in the fall of the following year. Trees in the interior, or at higher elevations, begin development later in the spring and complete development earlier in the fall than do trees growing in coastal or low-elevation regions.

Pollination, fertilization, and ovule and seed development occur in the second year. Many environmental and physiological factors within the tree, which are not fully understood, can affect differentiation and development of cone buds, and the subsequent development of cones and seeds. One of the most common causes for the absence of a cone crop is failure to initiate cone buds. As in many other conifers, hemlock cone crops are cyclic, occurring perhaps every three to four years, and less frequently at higher elevations where mountain hemlock commonly grows. A second weak link in the reproductive cycle is pollination, which can be especially poor at higher elevations, usually because of adverse weather conditions. Unpollinated ovules abort after the normal time of fertilization, forming empty seeds. Other ovules can abort before fertilization, for unknown causes, and produce flat seeds. Even pollinated ovules might not develop into filled or viable seeds because of embryo abortion or retarded embryo development.

Many factors that adversely affect cone initiation and cone and seed development can be avoided, overcome, or minimized if trees are grown in seed orchards. Furthermore, cone induction and enhancement can be easily attained in western hemlock through the use of gibberellins and water stress. In seed orchards frequent crops of abundant, high-quality seeds can be obtained from selected parent trees. Understanding the complete reproductive cycles of western and mountain hemlocks is a first, essential step in enhancing and controlling cone and seed production for reforestation of these two commercially important conifers.

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